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The Fellodistomidae (Digenea) of fishes from the northeast Atlantic

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Contents

Introduction

This is the third in a projected series of papers on the helminth-fauna of fishes from the northeast Atlantic region. The family discussed is the Fellodistomidae, a group restricted mainly to marine fishes, but occurring occasionally in freshwater fishes and as adults in marine invertebrates.

Materials and methods

The materials and methods used in this investigation are outlined in the first two papers in this series (Bray & Gibson, 1977; Gibson & Bray, 1977). In addition to the sources of material mentioned in these two papers, we have collected further material at Aberdeen in March–April 1977, and aboard MAFF RV *Cirolana* in NE Atlantic in 1978. In this report we have used the nomenclature and classification of fishes presented by Hureau & Monod (1973).

Bull. Br. Mus. nat. Hist. (Zool.) **37** (4) : 199–293 Issued 28 February 1980

Systematic section

Family FELLODISTOMIDAE Nicoll, 1909

Steringophoridae Odhner, 1911.
Xenoperidae Poche, 1926.
Monascidae Dollfus, 1947.

Diagnostic features. Body large to small; globular to elongate. Body-surface usually smooth; occasionally bearing spines or muscular ornamentation. Oral sucker subterminal; globular. Ventral sucker globular; large to small; in middle or anterior half of body. Prepharynx short to apparently absent. Pharynx well developed; globular to elongate. Oesophagus absent to long. Gut-caeca normally two; narrow to wide; reaching to testes or beyond; occasionally with single caecum (? opening into excretory vesicle). Testes two; oval to globular; entire or deeply lobed; symmetrical, oblique or tandem; in anterior or posterior hindbody; normally post-ovarian. Cirrus-sac usually well developed, occasionally absent; oval to claviform; containing seminal vesicle, pars prostatica, prostatic cells and ejaculatory duct. Seminal vesicle usually bipartite; occasionally globular or convoluted and tubular. Pars prostatica usually wide with filamentous lining; occasionally greatly reduced. Spermatophores may be produced. Ejaculatory duct usually wide and convoluted; occasionally small and narrow. Genital atrium short to long. Genital pore ventral; usually sinistral; in middle or posterior half of forebody. Ovary entire to multilobate; in hindbody; usually anterior to testes. Laurer's canal present. Uterine seminal receptacle usually present; canalicular seminal receptacle (see Gibson & Bray, 1979) occasionally present. Uterus normally reaching posteriorly to testes; bulk of uterus usually post-testicular. Eggs numerous; small; variable; operculate; egg-shell occasionally ornamented. Vitellarium follicular; typically in two lateral fields; occasionally amalgamated to form two oval masses; occasionally confluent medially. Excretory pore terminal; vesicle 'Y'- or 'V'-shaped, with anterior arms reaching to about level of pharynx. Parasitic in intestine, pyloric caeca, bile duct and gall-bladder of marine, and occasionally freshwater, teleosts; occasionally occurring as adults in molluscs (bivalves and gastropods).

A taxonomic history of the group

Nicoll (1909*a*) erected the subfamily Fellodistominae in the suborder Prosostomata Odhner, 1905, to include the two genera *Fellodistomum* Stafford, 1904, and *Steringophorus* Odhner, 1905. Two years later Odhner (1911*a*), in erecting the new family Steringophoridae, provided the first detailed concept of this group. In it he included *Steringophorus*, *Fellodistomum*, *Tergestia* Stossich, 1899, and four new genera, *Rhodotrema*, *Steringotrema*, *Haplocladus* and *Proctoeces*. The name Steringophorinae was used by Odhner to replace the name Fellodistominae, as he felt that it was more appropriate and, in addition to *Steringophorus* and *Fellodistomum*, he included *Rhodotrema* and *Steringotrema*. For the remaining genera, *Haplocladus*, *Proctoeces* and *Tergestia*, he erected the subfamily Haplocladinae. Woodcock (1912) first used the name Fellodistomidae, and Nicoll (1913) pointed out its priority to the appellation Steringophoridae.

The two subfamilies Steringophorinae [= Fellodistominae] and Haplocladinae were recognized by Fuhrmann (1928) and Issaitschikov (1928), the Steringophorinae having grown to include six genera and the Haplocladinae to include four genera. The next important developments were made by Dollfus (1952), who recognized four subfamilies, the Fellodistomatinae [*sic*], containing four genera with a pre-testicular uterus, the Steringophorinae, containing 14 genera with the uterus mainly post-testicular, the Monascinae Dollfus, 1947, containing five genera with the uterus distributed both anteriorly and posteriorly to the testes, and the Discogasteroidinae Srivastava, 1939, containing two genera with a number of characteristics including short caeca and a seminal receptacle. Cable (1953), using evidence from life-history studies, included the Fellodistominae, Haplocladinae, Tandanicolinae Johnston, 1927, and Gymnophallinae Odhner, 1905, in the Fellodistomatidae [*sic*]; but Yamaguti (1953*a*), although including 20 genera in the family, did not recognize any of the subfamilies. Skrjabin & Koval (1957), however, further subdivided the family into 11 subfamilies, the Fellodistomatinae [*sic*], the Discogasteroidinae, the

Haplocladinae, and eight new subfamilies, the Ancylocoeliinae, the Antorchiinae, the Lissolomatinae, the Markevitschiellinae, the Pyriformiinae, the Proctoecinae, the Tergestiinae and the Yamagutiinae. Yamaguti (1958) recognized 10 subfamilies, the Fellodistominae, the Monascinae, the Discogasteroidinae, the Antorchiinae, the Pyriforminae, the Tergestiinae, the Lissolomatinae, the Heterorchiinae Dollfus, 1950, and two new subfamilies, the Pentagramminae and the Symmetrovesiculinae [being unaware of Skrjabin & Koval's (1957) work, Yamaguti also considered that four of the other subfamilies were new]. Baer & Joyeux (1961), however, retained only four subfamilies, the Fellodistomatinae [*sic*], the Antorchiinae, the Gymnophallinae and the Heterorchiinae. Mehra (1963) recognized 9 subfamilies, synonymizing the Discogasteroidinae with the Fellodistominae and the Pentagramminae with the Antorchiinae. He also included the Baccigerinae Yamaguti, 1958, transferring it from the Cryptogonimidae Ward, 1917. Overstreet (1969) and Angel (1971) considered the Monodhelminthinae Dollfus, 1937, as a subfamily of the Fellodistomidae and, finally, Yamaguti (1971) recognized 15 subfamilies, the Baccigerinae, Proctoecinae, Parantorchiinae Yamaguti, 1958, Lintoniinae Yamaguti, 1970, Stenakrinae Yamaguti, 1970, and two new subfamilies, the Trigonocryptinae and the Infundibulostominae, being added to his earlier (1958) list. Yamaguti (1971) followed Travassos, Teixeira de Freitas & Bührnheim (1965) in giving family-status to the Monascinae and considered the Pentagramminae to be synonymous with the Baccigerinae.

It can safely be said that not since the work of Odhner (1911*a*) has a revision of the family been solidly based on a study of specimens of the genera involved. As can be seen from the brief summary presented above, much juggling of the subfamilies has occurred during the history of this family. This is not the place to attempt a complete reclassification of the group, being beyond the scope of this series. A detailed study of those forms from the northeast Atlantic region has, however, been undertaken. The following five subfamilies are, therefore, considered here: the Fellodistominae, the Baccigerinae, the Xenoperinae Poche, 1926, the Tergestiinae and the Monascinae.

Some comments on forms previously treated as fellodistomids

Certain genera, which at one time or another have been considered as fellodistomids, have been omitted from this study. *Ancylocoelium* Nicoll, 1912, was originally included in the Haplocladinae; but Nicoll indicated that its relationships are not straightforward and that its designation was provisional. In our opinion, its most satisfactory position is in the Monorchiidae Odhner, 1911. A close comparison of this genus with *Chrisomon tropicus* (Manter, 1940) as described by Kovaleva (1970*a*) from the same host may reveal that Nicoll (1912) misinterpreted certain features.

The Stenakrinae was included in the Fellodistomidae by Yamaguti (1970, 1971); but an examination of members of this subfamily has led us to believe that it is best placed in the Opecoelidae Ozaki, 1925. *Stenakron* Stafford, 1904, was not well known until studied by the Russian workers Strelkov (1960) and Mamaev, Parukhin & Baeva (1963). Prior to the latter work this genus was always considered an allocreadiid, but Mamaev *et al.* placed it in the Fellodistomidae. It has been confused with *Rhodotrema* Odhner, 1911, particularly by Russian workers: this confusion is discussed below (p. 245). Having studied *Stenakron vetustum* Stafford, 1904, *S. kerguelense* Prudhoe & Bray, 1973, *Anisorchis opisthorchis* Polyanski, 1955, and *Caudotestis nicolli* Issaitschikov, 1928, Bray (1979) was able to point out that the members of this subfamily differ from the Fellodistomidae in the following characters: I-shaped excretory vesicle; long claviform cirrus-sac containing single large sac-like seminal vesicle; small narrow pars prostatica; and long ejaculatory duct. Other normal characters of the Stenakrinae are unusual in the Fellodistomidae: these include large eggs, a pre-testicular uterus and vitelline fields confluent in the median line. It is also possible that the cercariae of *Stenakron* are microcercous and occur in gastropods, as in the case of the opecoelids; but the cercariae apparently lack a stylet (Chubrik, 1966). Gaevskaja & Kovaleva (1977) follow Prudhoe & Bray (1973) in including *Stenakron* in the Opecoelidae.

Another putative member of the Fellodistomidae is *Yamagutia anarhichae* Brinkmann, 1956, from the gall-bladder of *Anarhichas minor* from Iceland. This taxon is based upon a single well-flattened specimen, which, through the kindness of Dr F. Gudmundsson of the Museum of Natural History, Reykjavik, we have been able to examine. It appears to us to be a teratological specimen of the zoogonid *Deretrema pycnorganum* (Rees, 1953), which occurs commonly in the gall-bladder of this host off Iceland. A comparison with specimens of *D. pycnorganum* in the collections of the British Museum (Natural History) indicates that there is a great similarity in the alimentary system and the terminal genitalia. In addition, some of our specimens, especially the smaller ones, exhibit no tegumental spines, which, according to Brinkmann (1956), are also missing in *Y. anarhichae*. The 'opening of Laurer's canal', as described by Brinkmann, appears to be, in fact, the excretory pore which has been displaced onto the dorsal surface by pressure during fixation. We have no doubt, therefore, in considering *Yamagutia anarhichae* (the type-species of the genus *Prolateroporus* Yamaguti, 1971) to be a synonym of *D. pycnorganum*.

Aspects of biology

The fellodistomids have small eggs and, according to Cable (1974), miracidia with cilia confined to patches. The sporocysts develop in bivalve molluscs and the daughters normally give rise to motile cercariae. These cercariae are basically furcocercous, the excretory vesicle opening terminally on the furcae, if the latter are present. The tail, however, may be trichocercous and long, or much reduced and deciduous (see Cable, 1954). The metacercariae occur in amphipods, ctenophores and echinoderms, but in some instances the life-cycle may be telescoped, with the adults occurring in a gastropod or with the complete cycle occurring in the lamellibranch. Whilst this telescoping may occur as a general pattern in some species, other species occasionally occur as progenetic metacercariae in the second intermediate host. Apart from these examples, adult fellodistomids are found in the intestine or neighbouring organs of marine, and occasionally freshwater, teleosts. Some species exhibit a fairly rigid host-specificity, whilst others appear to be specific in part of their range and less specific in other parts. A common pattern of specificity is for the parasite to show a strong preference for a particular host species or group of species, but to occur occasionally, sometimes in an immature condition, in other hosts. The group is widespread in sub-polar, temperate and tropical waters and in both the shallows and the deeps.

Copulation is apparently reciprocal and involves the juxtaposition of the genital atria. In some species at least it involves the transfer of spermatozoa encased in fibrous spermatophores.

Key to the subfamilies of the Fellodistomidae in the northeast Atlantic

1 Caecum single (? unites with excretory vesicle) . . . . . **MONASCINAE** (p. 268)
– Caeca double 2
2 Ring of conical papillae surrounding oral sucker; ridges on lateral surface of forebody; cirrus-sac bipartite; pharynx elongate . . . . **TERGESTIINAE** (p. 274)
– Body-surface lacking ornamentation; cirrus-sac oval to globular; pharynx oval 3
3 Genital atrium long, narrow; seminal vesicle coiled, tubular; cirrus-sac surmounted by muscular papilla . . . . **XENOPERINAE** (p. 259)
– Genital atrium short to long; seminal vesicle bipartite 4
4 Seminal vesicle almost fills cirrus-sac; genital atrium long, narrow; vitellarium in 2, or a few, compact bunches of follicles; Laurer's canal opening at or near posterior extremity; canalicular seminal receptacle present; ovary post- or inter-testicular . . **BACCIGERINAE** (p. 248)
– Seminal vesicle small relative to size of cirrus-sac; genital atrium short, wide; vitellarium 2 (occasionally 4) lateral follicular fields; Laurer's canal opening dorsal to gonads; uterine seminal receptacle present; ovary pre-testicular . . . **FELLODISTOMINAE** (p. 202)

Subfamily **FELLODISTOMINAE** Nicoll, 1909

Steringophorinae Odhner, 1911.
Lissolomatinae Skrjabin & Koval, 1957.
Markevitschiellinae Skrjabin & Koval, 1957.

DIAGNOSTIC FEATURES. Body large and robust to small. Body-surface smooth. Ventral sucker usually larger than oral sucker, occasionally smaller; in middle of body or in anterior half. Pharynx globular to oval. Oesophagus absent, short or long. Caeca narrow to wide; reaching to testes or beyond and almost to posterior extremity. Testes in anterior hindbody; post-ovarian. Cirrus-sac well developed; oval to claviform; containing many prostatic gland-cells. Pars prostatica wide; straight or gently curved. Ejaculatory duct wide; pocketed. Spermatophores occasionally seen. Genital atrium small. Genital pore in mid-forebody; sinistral to median line. Ovary entire to multilobate; usually anterior to right testis. Laurer's canal and uterine seminal receptacle present. Uterus usually reaching posteriorly to testes, but does not extend into post-testicular region in type-genus. Metraterm joins genital atrium from left. Eggs numerous; operculate; small; often variable; egg-shell may be ornamented. Vitellarium follicular; in two (occasionally four) lateral fields; in fore- and/or hindbody. Excretory pore terminal; vesicle 'V'- or 'Y'-shaped; with arms reaching to level of pharynx or oral sucker. Parasitic in intestine, pyloric caeca, bile duct and gall-bladder of marine teleosts.

COMMENT. The Steringophorinae is retained as a distinct subfamily by Dollfus (1952) on the basis of the distribution of the uterus; but the present study indicates that the type-species of *Fellodistomum* Stafford, 1904, and *Steringophorus* Odhner, 1905, are similar, and that there is a form, *Steringophorus agnotus* (Nicoll, 1909), which is in some ways intermediate. We, therefore, consider it unnecessary to distinguish the Steringophorinae. The other synonyms listed, the Lissolomatinae and the Markevitschiellinae, are not well known and are not represented in our region; but it appears that *Lissoloma* Manter, 1934, is close to *Steringophorus* and *Markevitschiella* Skrjabin & Koval, 1957, is close to *Steringotrema* Odhner, 1911.

This subfamily, as represented below, is a fairly homogeneous group, and it is noticeable, for example, how similar the cirrus-sac and contents are in virtually all of the species described. The typical arrangement is well-figured and described by Nicoll (1909*a*, p. 466) and Odhner (1911*a*, p. 101). The terminology of the distal part of the male-duct is rather confusing, for as the ejaculatory duct is muscular with irregular, shallow diverticula and muscular lobations, it has been considered to be the genital atrium or sinus by some authors. These diverticula have also been termed the 'atrial diverticle' by Yamaguti (1940) in *Pseudosteringophorus* and 'atrial sac' by Manter (1947) and Armstrong (1974) in *Megalomyzon* and a number of fellodistomines, respectively. Nicoll (1909*a*), for example, states, 'at first sight the genital sinus appears to be of great size, but this is due to a wide expansion of the ductus ejaculatorius. In reality the genital sinus is comparatively small'. Our observations agree with those of Nicoll: the ejaculatory duct in relaxed specimens, we found, is always included within the cirrus-sac. The pars prostatica is a wide, straight or slightly curved vesicular structure and is lined with numerous narrow filaments which often extend into the lumen of the ejaculatory duct. These filaments appear to be involved in the formation of a fibrous spermatophore. The seminal vesicle is normally bipartite, but one or both parts may be reduced when the spermatozoa have been ejected.

The ovary in this subfamily appears in two basic forms. *Fellodistomum* and *Steringophorus* each has a distinctive acinous, multilobate ovary, while in the other genera the ovary has a smooth surface, having either a more or less globular or a trilobed shape.

A comment should be made on the unreliability of egg-measurements as taxonomic criteria in this group. As can be seen from *Steringophorus furciger* and *Steringotrema pagelli* (Tables 2 & 7) in particular, the egg-length can vary considerably, and it is apparent that in these two species at least the literature suggests that there may be an overall bimodal distribution of egg-sizes. The latter phenomenon may, however, be the result of authors measuring eggs at different stages of development.

Key to the genera of the Fellodistominae from the northeast Atlantic

1 Uterus reaching posteriorly to testes; hindbody at least as long as forebody 2
– Uterus not reaching posteriorly to testes; body almost globular; ventral sucker large . . . . *FELLODISTOMUM* Stafford, 1904 (p. 204)
2 Excretory vesicle 'Y'-shaped 3
– Excretory vesicle 'V'-shaped 4

3 Ovary multilobate; caeca reach to level of testes or, more usually, beyond; posterior limit of vitelline follicles lies posterior to anterior margin of ventral sucker; prepharynx small, indistinct . . . . **STERINGOPHORUS** Odhner, 1905 (p. 210)
– Ovary trilobed; caeca reach to about level of anterior margin of testes; vitelline follicles entirely in forebody; prepharynx small, distinct . . . . **OLSSONIUM** gen. nov. (p. 228)
4 Body stout; vitellarium extending into forebody and posteriorly as far as testes, mainly in lateral fields; caeca reaching to region of testes . . **STERINGOTREMA** Odhner, 1911 (p. 231)
– Body elongate; vitellarium confined to hindbody, reaching well posteriorly to testes; caeca extend almost to posterior extremity . . . . . . **PRUDHOEUS** gen. nov. (p. 245)

Genus *FELLODISTOMUM* Stafford, 1904

DIAGNOSTIC FEATURES. Body large; robust. Ventral sucker large; larger than oral sucker; globular; at middle of body or just posterior to it. Prepharynx short. Pharynx well developed; globular. Oesophagus absent. Caeca wide; reaching close to posterior margin of testes. Testes two; symmetrical; oval; close to posterior extremity. Cirrus-sac claviform. Seminal vesicle bipartite. Pars prostatica wide; surrounded by gland-cells. Ejaculatory duct wide; diverticulate. Genital atrium small. Genital pore close to ventral sucker; sinistrally submedian. Spermatophores may be present. Ovary multilobate; just anterior to right testis. Uterus not extending posteriorly to testes or small portion only posterior to testes [especially in flattened specimens]; bulk of uterus dorsal and lateral to ventral sucker. Eggs numerous; small; with smooth shells. Vitelline follicles in two lateral fields; lateral to and reaching just anteriorly to ventral sucker. Excretory vesicle 'Y'-shaped; stem reaching forward to anterior margin of testes; arms reaching to pharynx. Parasitic in gall-bladder of marine teleosts (Anarhichadidae).

TYPE-SPECIES. *Fellodistomum fellis* (Olsson, 1868) (by subsequent designation: Nicoll, 1909*a*: 471).

COMMENT. The present concept of the genus *Fellodistomum* includes only the large, almost globular type-species in which little or none of the uterus lies posteriorly to the testes. Our reasons for distinguishing *Steringophorus* are discussed below (p. 210). Eighteen species have, at one time or another, been assigned to this genus. These are:

(1) *F. agnotum* Nicoll, 1909, which is herein considered to be a species of *Steringophorus* (see p. 217).
(2) *F. anarhichaelupi* (Rathke, 1799) Dollfus, 1968; Dollfus (1968) used this name as a senior synonym of *F. incisum* (Rudolphi, 1809). We do not consider that either Rathke's (1799) or Rudolphi's (1809) descriptions are recognizable as species of *Fellodistomum* (see p. 209).
(3) *F. breve* Ching, 1960 (emend. Yamaguti, 1971), herein considered a species of *Steringophorus* (see p. 211).
(4) *F. fellis* (Olsson, 1868) Nicoll, 1909; type and only valid member of the genus.
(5) *F. furcigerum* (Olsson, 1868) Yamaguti, 1953; type-species of the genus *Steringophorus* (see p. 212).
(6) *F. incisum* (Rudolphi, 1809) Stafford, 1904; unrecognizable (see p. 209).
(7) *F. lethrini* (Gupta, 1956) Yamaguti, 1971; recorded from *Lethrinus* sp. from the Gulf of Manaar off India, this species was originally placed in *Steringophorus*. Yamaguti (1971), in addition to including it in *Fellodistomum* (p. 70), made it the type-species of a new genus, *Guptatrema*, which he placed in the Callodistomidae Odhner, 1910 (p. 118). Although certain marine callodistomids, e.g. *Callodistomoides* Yamaguti, 1970 (see p. 211), are difficult to distinguish from fellodistomids, *Guptatrema* appears to have characters not usually associated with the latter group, such as a long, narrow cirrus-sac, a large seminal receptacle and caeca reaching to the posterior extremity. Its position is, therefore, uncertain; but it resembles, superficially at least, *Paracryptogonimus ovatus* Yamaguti, 1952, from an unknown marine fish from off the Celebes (Yamaguti, 1952) and *Pomadasys hasta* from the Bay of Bengal (Madhavi, 1976) and *Paracryptogonimus rostratus* Nagaty & Abdel Aal, 1961, from *Lethrinus rostratus* in the Red Sea, species which are considered synonyms by Manter (1963).

(8) *F. magnum* (Manter, 1934) Yamaguti, 1953, herein considered a species of *Steringophorus* (see p. 211).

(9) *F. mendezi* Sogandares-Bernal, 1955, from the intestine of a freshwater fish, *Brachyrhaphis episcopi* in Gatun Lake, Panama. The uterus of this worm contains an average of only 10 eggs, and it is figured as possessing a considerable proportion of its uterus in the post-testicular field. As it is described mainly from a single specimen, its status is in some doubt.

(10) *F. melanostigmum* Noble & Orias, 1975, herein considered a species of the genus *Steringophorus* (see p. 211).

(11) *F. ovatum* (Price, 1934) Yamaguti, 1971; this is possibly a species of the genus *Bacciger* (see p. 249).

(12) *F. phrissovum* Aldrich, 1961, herein considered a species of the genus *Steringotrema* (see p. 232).

(13) *F. preovaricum* Caballero y C., Bravo Hollis & Grocott, 1952, from the intestine of *Galeichthys seemanni* off the Pacific coast of Panama. This species was made the type of a new genus, *Allofellodistomum*, by Yamaguti (1971). The location of the ovary in the forebody appears to justify this action, although the spinose body-surface suggests that it may not be a fellodistomid.

(14) *F. profundum* (Manter, 1934) Yamaguti, 1953, herein considered to be a species of the genus *Steringophorus* (see p. 211).

(15) *F. rotundum* (Manter, 1954) Yamaguti, 1971, herein considered to be a member of the genus *Steringotrema* (see p. 232).

(16) *F. sebastodis* Yamaguti & Matumura, 1942, herein considered to be a species of the genus *Steringophorus* (see p. 211).

(17) *F. saviniense* Dyk & Dykova, 1964, from the gall-bladder of *Salmo trutta* and *Thymallus thymallus* in the River Savinja, Yugoslavia. It seems likely that this species belongs to the zoogonid genus *Pseudochetosoma* Dollfus, 1951, which contains species from the gall-bladder of freshwater fishes in central Europe (Kakacheva-Avramova, 1966*a*, 1966*b*).

(18) *F. thapari* Srivastava & Ghosh, 1968; a synonym of *F. fellis.*

Fellodistomum fellis (Olsson, 1868) Nicoll, 1909

Distoma fellis Olsson, 1868.
Distoma incisum Rudolphi of van Beneden (1871).
Fellodistomum incisum (Rudolphi) of Stafford (1904) in part (?).
(?) *Cercaria limae* Nicoll & Small, 1909.
(?) *Metacercaria limae* (Nicoll & Small) James, Sannia & Bowers, 1977.
Adolescaria ophiurae Tauson, 1917.
Fellodistomum thapari Srivastava & Ghosh, 1968.

TYPE-HOST AND LOCALITY. *Anarhichas lupus*, Varberg, Sweden.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas lupus [gall-bladder] Iceland (see Rees, 1953: 15). BM(NH) 1976.4.8.179.
—— [gall-bladder] Herdla, Norway (July, 1971). Material of J. Thulin.
—— [gall-bladder] Eldey Bank, off Reykjanes, Iceland (64°N, 24°W; depth 148–152 m; May, 1974). BM(NH) 1977.3.1.1–20.
—— [gall-bladder] Orkney Islands, Scotland (59°N, 04°W; depth 164–172 m; July, 1976). BM(NH) 1977.3.1.21–40.
—— [gall-bladder] Moray Firth, Scotland (58°N, 02°W; depth 164 m; July, 1976). BM(NH) 1977.3.1.21–40.

(b) From elsewhere

Anarhichas denticulatus [gall-bladder] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.15.202–203.

Anarhichas lupus [gall-bladder] Locality unknown; donated by Zoological Museum, Amsterdam. BM(NH) 1946.12.20.1–20.

—— [gall-bladder] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.15.186–200.

Anarhichas minor [gall-bladder] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.15.201.

(ii) NE Atlantic records from the literature

Anarhichas lupus [gall-bladder & intestine] Varberg, Sweden (July, Aug.). Olsson (1868 : 44; as *Distoma fellis*).

—— [gall-bladder & intestine] Belgian coast. van Beneden (1871 : 48; as *Distoma incisum*);

—— [gall-bladder] North Sea (Feb., 1893). Jacoby (1899 : 12; as *Distomum fellis*).

—— [gall-bladder] Northumberland, England. Lebour (1908*a* : 36; as *Distomum fellis*).

—— [gall-bladder] St Andrews, Fife, Scotland. Nicoll (1909*a* : 458).

—— [gall-bladder] East coast of Iceland (66°N, 13°W; depth 119 m; Aug. 1948). Rees (1953 : 15).

—— [gall-bladder] Reykjavik, Neskaupstadur & Húsavík, Iceland (June, July 1955). Brinkmann (1956 : 20).

Anarhichas minor [gall-bladder] Neskaupstadur & Húsavík, Iceland (July, 1955). Brinkmann (1956 : 20).

—— [gall-bladder] Umîvik, East Greenland (July, 1959). Brinkmann (1975 : 51).

ASPECTS OF BIOLOGY. Records of intermediate hosts in the NE Atlantic:

(a) First intermediate host

Nil.

(b) Second intermediate host

Ophiura albida [stomach] Kristineberg, Sweden. Mortensen (1920 : 67; identification by T. Odhner).

[?] *Lima hians* [mantle] Millport, Firth of Clyde, Scotland. Nicoll & Small (1909 : 241; as *Cercaria limae*).

[?] *Macoma baltica* [?] Burry Inlet, South Wales. James, Sannia & Bowers (1977 : 13; as *Metacercaria limae*).

The life-history of this species has been studied by Chubrik (1952, 1966) in the Barents Sea. This author states that the sporocysts develop in the bivalve *Nucula tenuis* and the daughters contain 7–10 cercariae. These cercariae are non-oculate, brevifurcate and distomatous, possessing an almost 'V'-shaped excretory vesicle with its base forming a reservoir. The tail is broad and flat. The metacercariae are found in the digestive tract of echinoderms of the genus *Ophiura* and progenesis occasionally occurs. *Adolescaria ophiurae*, described by Tauson (1917) from *Ophiura sarsi* in the Barents Sea, is so similar to the *Fellodistomum* metacercariae described by Chubrik that there can be little doubt of its identity with *F. fellis*. A similar worm, *Cercaria limae*, was described from the gaping file-shell bivalve, *Lima hians*, by Nicoll & Small (1909). Single encysted specimens were found loosely attached to the underside of the mantle-edge, projecting into the mantle-cavity of two file-shells. Nicoll & Small considered that the evidence strongly suggested that they were *F. fellis;* but that they could also belong to a species of *Steringophorus*, particularly as *Anarchichas lupus* was rare in their area. This same worm has also been found recently by James *et al*. (1977) in the Baltic tellin *Macoma baltica* from south Wales.

This species normally occurs in the gall-bladder of anarhichadid fishes, sometimes in great numbers (over 4000, according to Polyanski, 1955); but it is occasionally found in the intestine or urinary bladder (Olsson, 1868; van Beneden, 1871; Polyanski, 1955). In addition, Polyanski (1955) found immature specimens in the intestine and gall-bladder of the plaice *Pleuronectes platessa*, and Srivastava & Ghosh (1968) record their *Fellodistomum thapari* from the gall-bladder of the anglerfish *Lophius piscatorius* and from the intestine of *Anarhichas lupus*. A study of the literature indicates that *F. fellis* is restricted to the northern Atlantic Ocean and the Barents Sea.

We found two specimens which are apparently in the act of copulation (Fig. 1d). The genital pores are juxtaposed with the forebodies of each worm at an acute angle to each other. When separated, structures interpreted as being spermatophores were seen, apparently having been expelled from the genital pore of both worms, lying close to these pores. In sections, the fibrous coat of the spermatophore can be traced back to the cells lining the pars prostatica (Fig. 2). The bipartite seminal vesicle in one of this pair which was sectioned contained very few spermatozoa. It seems likely, therefore, that sperm-transfer takes place via the metraterm and not via Laurer's canal.

Previous descriptions. Olsson (1868 : 44; as *Distoma fellis*); Jacoby (1899 : 12; as *Distomum fellis*); Nicoll (1909*a* : 458); Miller (1941 : 43); Rees (1953 : 15); Polyanski (1955 : 20); Srivastava & Ghosh (1968 : 46; as *F. thapari*).

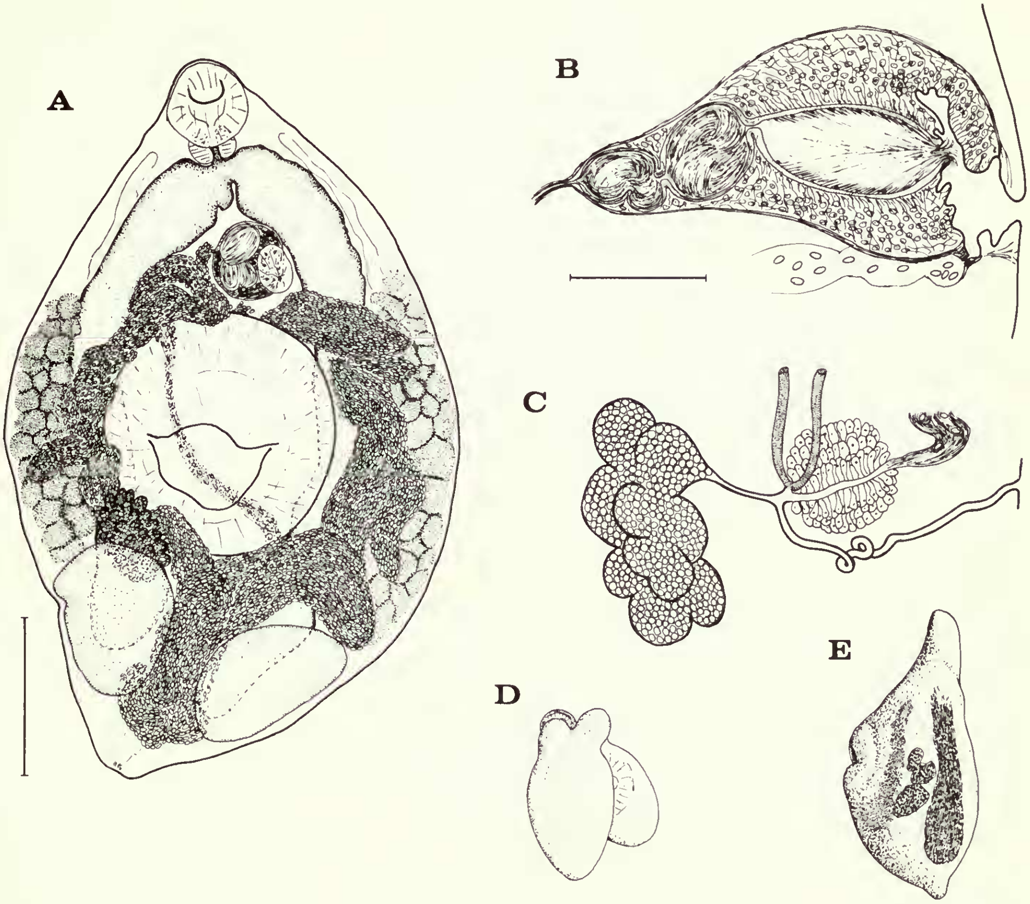

Fig. 1 *Fellodistomum fellis:* (a) slightly flattened whole mount; (b) cirrus-sac; (c) diagram of female proximal genitalia; (d) two worms in copulation (free-hand sketch); (e) lateral view of fixed but unflattened worm (free-hand sketch). Bar scales: a = 1 mm; b = 0·25 mm.

Description (Figs 1 & 2). This description is based upon 38 whole-mounted and three serially sectioned specimens which represent a wide range of sizes and states of maturity. The dimensions of these worms, in addition to some measurements from the literature, are included in Table 1.

The adult worms are stout (Fig. 1e) and are almost subglobular with an anterior protuberance carrying the oral sucker in addition to a small posterior protuberance. The body-wall is thin and unarmed. The subglobular *oral sucker* opens subterminally, and the large, globular *ventral sucker* is deeply embedded in the middle of the body (Fig. 1a). The ventral sucker is invariably much broader than the oral sucker, in the ratio of 1 : 1·5–3·0, with a distinct tendency for the ratio in

Table 1 Dimensions of *Fellodistomum fellis* from the present material and from the literature

Authority	Jacoby (1899)	Nicoll (1909*a*)	Rees (1953)	Present material
Name used	*Distomum fellis*	*Fellodistomum fellis*	*Fellodistomum fellis*	*Fellodistomum fellis*
Hosts	*Anarhichas lupus*	*Anarhichas lupus*	*Anarhichas lupus*	see text
Locality	North Sea	Scotland	Iceland	see text
Length (mm)	2–2·5	2·5–3·3	2·5–3·3*	0·97–3·7*
Breadth (mm)	1	1·1–1·6	1·1–1·8	0·38–2·44
Length : forebody ratio	(1 : 0·41)	–	–	1 : 0·23–0·48
Oral sucker (mm)	0·36 dia.	0·40–0·45 dia.	0·40–0·45	0·18–0·56 × 0·22–0·67
Ventral sucker (mm)	0·88 dia.	0·9–1·0 dia.	0·90–1·50	0·34–1·62 × 0·33–1·84
Sucker-ratio	(1 : 1·9)	–	1 : 2·25–3	1 : 1·5–3·0
Pharynx (mm)	0·22 dia.	0·16–0·21 long	0·18–0·21	0·13–0·27 × 0·13–0·28
Cirrus-sac (mm)	0·29 × 0·23	–	–	0·92 × 0·39†
Testes (mm)	–	0·45 × 0·19	–	0·10–0·80 × 0·09–0·60
Ovary (mm)	–	–	–	0·42 × 0·22†
Eggs (μm)	40 × 20	42 × 23	42–43 × 23–24	37–48 × 19–29

* Some measurements from flattened specimens.
† Measured from sections.

the larger worms to be greater than in the smaller. The oral sucker is connected by a short prepharynx (visible only in sections) to a globular *pharynx*. There is no oesophagus as the intestine divides immediately on leaving the pharynx and forms two wide, but thin-walled, caeca, which are almost invariably filled with the semi-digested remains of blood-cells. This opaque mass often obscures much of the internal details of the worm in whole-mounts. The caeca, which are apparently lined with squamous epithelium, run in the dorso-lateral fields and terminate blindly at the level of the testes.

The *excretory pore* lies terminally and leads via a short, narrow duct into the wide stem of the excretory vesicle, which reaches to the anterior margin of the testes. At this point narrow arms arise which pass dorso-laterally to the ventral sucker and expand slightly in the forebody. They terminate laterally at the level of the pharynx.

The irregular but more or less oval *testes* lie symmetrically close to the posterior extremity. The two vasa efferentia unite to form the seminal vesicle immediately after passing through the base of the thin-walled *cirrus-sac*. The latter structure lies just anteriorly to the ventral sucker. As it lies more or less perpendicularly to the ventral surface, the measurement for it given in Table 1 is taken from longitudinal sections. It is claviform in shape, narrowing proximally, and contains, in addition to a bipartite seminal vesicle, a wide pars prostatica and a wide, irregular ejaculatory duct (Fig. 1b). The proximal part of the seminal vesicle may be slightly coiled, and occasionally one or both parts may be reduced to a narrow duct, especially when a spermatophore is present. The wider distal part of the cirrus-sac contains the dilate pars prostatica which is surrounded by a dense mass of gland-cells and lined by numerous filamentous projections. These projections extend forward into the ejaculatory duct through a narrow opening and appear to be involved in the formation of the wall of the spermatophore (Fig. 2). The ejaculatory duct is large and may be mistaken for a genital atrium. Its wall is strongly muscular and forms numerous irregular pockets and lobes. The genital atrium itself is small and opens, via the genital pore, in the posterior region of the forebody just to the left of the median line.

The multilobate *ovary* lies close to the anterior margin of the right testis. From it a narrow oviduct passes dorsally, leading to a diffuse Mehlis' gland. Laurer's canal, which opens dorsally at about the level of the ovary, and a minute common vitelline duct open into the oviduct just prior to its entry into Mehlis' gland (Fig. 1c). The initial coils of the *uterus* form a uterine seminal receptacle, there being no other seminal storage organ in the female part of the reproductive

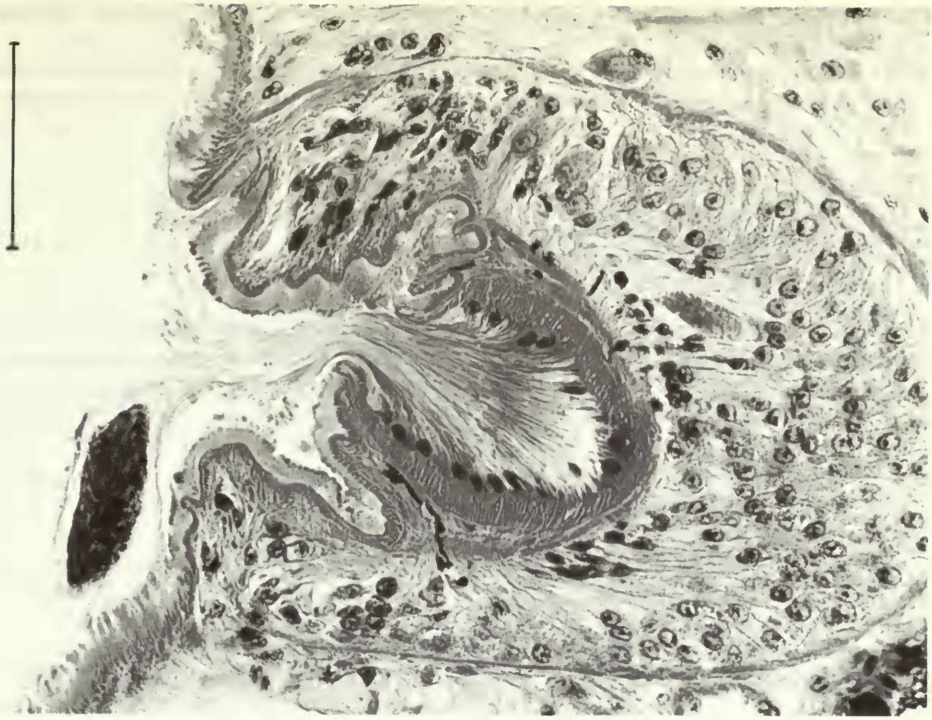

Fig. 2 Photomicrograph of section showing spermatophore production in *Fellodistomum fellis*. Bar scale: =0·1 mm.

system. The uterine coils extend posteriorly between, or fractionally beyond, the testes; but the great bulk of the uterus occurs between the testes and the cirrus-sac, especially around the ventral sucker. The distal extremity of the uterus, which is thin-walled and wide, enters the genital atrium posteriorly through a muscular sphincter (Fig. 1b). The numerous eggs which fill the uterus are operculate and possess a smooth shell. The vitellarium consists of a number of irregular follicles of varying sizes, which are packed tightly in lateral fields between the anterior margins of the testes and the anterior margin of the ventral sucker or the cirrus-sac. There are two main lateral vitelline ducts at the level of the ovary which pass medially and unite to form the short common vitelline duct immediately prior to uniting with the oviduct.

Discussion. *Distomum fellis* of Olsson (1868) is the earliest name that can unequivocally be used for this species. Older names, such as *Distoma anarhichaelupi* Rathke, 1799, and *D. incisum* Rudolphi, 1809, from the stomach of *Anarhichas lupus*, cannot be compared as the descriptions are totally inadequate. In addition, these names have fallen out of use since Nicoll (1909*a*), who discussed their validity at some length, came to the same conclusion. The figure of *Distoma incisum* produced by van Beneden (1871) strongly suggests that he was dealing with *F. fellis:* we have, therefore, included this as a synonym. The genus *Fellodistomum* was initially erected by Stafford (1904) based on his very brief description of '*F. incisum*'; but his specimens were redescribed by Miller (1941), who came to the conclusion that they were *F. fellis*.

Srivastava & Ghosh (1968) described a new species, *F. thapari*, from the gall-bladder of *Lophius piscatorius* and the intestine of *Anarhichas lupus* from an unknown locality [neither of these two fishes occur outside the North Atlantic region or, in the case of *A. lupus*, the Arctic Ocean; the material came from the collection of the late Dr G. S. Thapar]. There appears to be no reason to consider this species distinct from *F. fellis*. Three of the four differentiating features mentioned by these authors were probably produced by the flattening which appears to have been carried out on their specimens. The other feature, the sucker-ratio, lies in the middle of the range of the present material.

Fellodistomum agnotum Nicoll, 1909, was considered by Dawes (1947) to be a further synonym of *F. fellis*; but in this work we consider this form to be a species of *Steringophorus* (see p. 219).

Genus *STERINGOPHORUS* Odhner, 1905

Leioderma Stafford, 1904, *nec* Willemoes-Suhm, 1873.
Callodistomoides Yamaguti, 1970.
Abyssotrema Campbell, 1975.

DIAGNOSTIC FEATURES. Body large; deep-bodied to dorso-ventrally flattened. Ventral sucker usually larger than oral sucker; in anterior half of body. Prepharynx short or apparently absent. Pharynx well developed; globular. Oesophagus absent to long. Caecal bifurcation anterior to or at level of genital pore; caeca wide to narrow; reaching to testes, to about middle of post-testicular region or occasionally beyond. Testes oval, indented or deeply lobed; symmetrical to tandem. Cirrus-sac oval. Seminal vesicle bipartite. Pars prostatica wide; surrounded by gland-cells. Ejaculatory duct wide; diverticulate. Genital atrium small. Spermatophores may be present. Genital pore close to anterior margin of ventral sucker; sinistral to median line. Ovary multilobed; just pre-testicular. Uterus mainly coiled posteriorly to testes. Eggs numerous; small; shells occasionally ornamented. Vitelline follicles in two lateral fields between level of caecal bifurcation and level just posterior to testes. Excretory vesicle 'Y'-shaped; stem reaching to between middle of post-testicular region and about level of testes; arms extending into forebody. Parasitic in intestine (occasionally body-cavity, gall-bladder, bile-ducts, etc.) of marine teleosts.

TYPE-SPECIES. *Steringophorus furciger* (Olsson, 1868) (by original designation).

COMMENT. Yamaguti (1971) considers that *Fellodistomum* is an immature form of *Steringophorus* on the basis that the distribution of the uterus in the former genus does not extend into the post-testicular region. He presents this argument to support his belief that *Steringophorus* is a synonym of *Fellodistomum* which he first propounded in 1953. Our studies have shown, however, that even in immature specimens of *Steringophorus*, the primordium of the uterus extends into the post-testicular field. This condition is illustrated by Polyanski (1955, fig. 21B) in *Steringophorus furciger*, and we have seen it both in that species and in *S. agnotus* (Nicoll, 1909), the species of this genus which is considered to be most similar to *Fellodistomum*. In fact this difference between the genera is even more distinct because the pre-testicular part of the uterus in *Steringophorus* only fills with eggs to any significant extent in the older and larger specimens. In *Steringophorus* the post-testicular part of the uterus takes up a variety of forms, being, for example, a single convoluted loop in *S. agnotus*, a pair of lateral convoluted loops in *S. blackeri* Bray, 1973, and a complex arrangement filling much of the hindbody in *S. furciger*.

We have included the genus *Abyssotrema* Campbell, 1975, as a synonym of *Steringophorus*. Campbell (1975) placed this genus in the subfamily Monascinae, which he distinguished from the Fellodistominae by the position of the cirrus-sac ('preacetabular' in the Fellodistominae), the configuration of the testes ('symmetrical' in the Fellodistominae) and the position of the vitellarium ('preacetabular or rarely in acetabulotesticular zone' in the Fellodistominae). As can be seen from the present work, only the statement concerning the testicular configuration appears to be valid. Campbell also states that the fellodistomines (along with the Heterorchiinae) typically possess an ovary with a smooth margin, but again the present work shows that this is not the case. In fact *Abyssotrema* is similar to the known species of *Steringophorus*, differing significantly only in the configuration of the testes, which on its own does not seem to be a character of generic importance.

Campbell (1975) also compared *Abyssotrema* with the members of the Heterorchiinae, i.e. *Heterorchis* Baylis, 1915; *Mesolecitha* Linton, 1910; and *Elopsium* Fischthal & Thomas, 1972. *Heterorchis*, which occurs in lung-fishes and anurans in Africa, differs considerably from *Abyssotrema*, and from other fellodistomids, in many features and is probably best considered as a member of the Plagiorchiidae Lühe, 1901 (see Prudhoe & Bray, in press). *Mesolecitha* differs from *Abyssotrema*, and other fellodistomids, in possessing a spiny body-surface, a more elongate cirrus-sac, a dextral genital pore and a sinistral ovary (Linton, 1910; Fischthal & Thomas, 1968), although Manter (1947) could not confirm that spines were present on the body-surface and found the genital pore to be sinistral: he also found spines on the cirrus and metraterm. *Mesolecitha* also differs from *Abyssotrema* in having an entire ovary and a tendency for the vitelline fields to fuse medially. Campbell considered the genus most similar to *Abyssotrema* to be *Elopsium* Fischthal & Thomas, 1972 (syn. *Protomonascus* Thulin, 1973; see Thulin, 1974). It differs in the shape of the cirrus-sac, the coiled, tubular nature of the seminal vesicle, the narrow pars prostatica, the smaller ejaculatory duct, the longer caeca, the more posterior and more oblique position of the testes, the gonads widely separated by coils of the uterus and the more extensive vitellarium. The systematic position of *Elopsium* is not straightforward, but it does appear to be a fellodistomid.

Of the 14 species which have been assigned to the genus *Steringophorus* 11 are herein considered valid. They are:

(1) *Steringophorus agnotus* (Nicoll, 1909) Dollfus, 1952 (see p. 217).
(2) *S. brevis* (Ching, 1960) n. comb; described as *Fellodistomum brevis* from a single specimen taken from the intestine of the pleuronectid fish *Microstomus pacificus* at Friday Harbour, Washington State, USA. It possesses post-testicular uterine coils, a short oesophagus and other characters which indicate that it is a species of *Steringophorus*.
(3) *S. blackeri* Bray, 1973 (see p. 220).
(4) *S. foliatus* (Yamaguti, 1970) n. comb.; described as *Callodistomoides foliatus* from the intestine of *Emmelichthyops* sp. off Hawaii. It possesses lobed testes and is, therefore, similar to *S. thulini* sp. nov., but the caeca reach almost to the posterior extremity. Yamaguti (1970) described 'well-sclerotized gonotyles' which are apparently the irregularities in the wall of the ejaculatory duct which are seen in many fellodistomines. The cirrus-sac, therefore, exhibits a typical *Steringophorus* arrangement (see Yamaguti, 1970, Fig. 53B).
(5) *S. furciger* (Olsson, 1868) Odhner, 1905; type-species of the genus (see p. 212).
(6) *S. magnus* Manter, 1934; described from the intestine of an unidentified eel-like fish off Florida.
(7) *S. melanostigma* (Noble & Orias, 1975) n. comb., described as *Fellodistomum melanostigmum* from the intestine of *Melanostigma pammelas* off southern California. It is similar to *S. furciger* and to three of the other species from deeper waters, i.e. *S. blackeri*, *S. magnus* and *S. profundum* Manter, 1934. We have emended the suffix on the specific name.
(8) *S. pritchardae* (Campbell, 1975) n. comb. (see p. 223).
(9) *S. profundum* Manter, 1934; described from the intestine of *Argentina striata* off Florida.
(10) *S. sebastodis* (Yamaguti & Matumura, 1942) Dollfus, 1952; described as *Fellodistomum sebastodis* from the gall-bladder of *Sebastodes* spp. in the northern Pacific Ocean. This species has a number of characteristics in common with *S. agnotus*.
(11) *S. thulini* sp. nov. (see p. 226).

The three species not considered to belong to *Steringophorus* are:

(1) *S. cluthense* Nicoll, 1909; the type-species of the genus *Steringotrema* and a synonym of *Steringotrema pagelli* (see p. 234).
(2) *S. lethrini* Gupta, 1956; a species of doubtful status (see *Fellodistomum lethrini*, p. 204).
(3) *S. ovacutus* Lebour, 1908; herein considered a species of *Steringotrema* (see p. 242).

Key to the species of *Steringophorus* recorded from the northeast Atlantic

- Vitellarium partly in forebody; caeca reach back to level of testes or only just beyond; post-testicular region of uterus a single convoluted loop (occasionally a few loops) . . . . **S. agnotus** (Nicoll, 1909) (p. 217)
- Vitellarium not reaching into forebody; caeca reaching beyond testes up to half-way along post-testicular field; post-testicular region of uterus composed of two to many convoluted loops . 2

2 Testes tandem; bifurcation of excretory vesicle in middle of post-testicular region . . . . ***S. pritchardae*** (Campbell, 1975) (p. 223)

– Testes symmetrical to oblique; bifurcation of excretory vesicle further forward than middle of post-testicular region 3

3 Vitellarium not reaching posteriorly to testes, with closely packed irregular follicles; uterus irregularly coiled across centre of hindbody; eggs with smooth shells 4

– Vitellarium reaching just posteriorly to testes, follicles short and tubular to globular; uterus coiled in two (occasionally one) lateral, convoluted loops in post-testicular region, with significant part of hindbody lacking coils of the uterus; egg-shells ornamented with tubercles . . . . ***S. blackeri*** Bray, 1973 (p. 220)

4 Testes with smooth or slightly indented margins; sucker-ratio 1 : 1·5–2·3; eggs 42–54 (usually 46–52) (possibly up to 68) µm long; large ejaculatory duct, small seminal vesicle . . . . ***S. furciger*** (Olsson, 1868) (p. 212)

– Testes deeply lobed; sucker-ratio 1 : 1·2–1·75; eggs 36–43 (usually 38–42) µm long; small ejaculatory duct, large seminal vesicle . . . . . . ***S. thulini*** sp. nov. (p. 226)

Steringophorus furciger (Olsson, 1868) Odhner, 1905

Distoma furcigerum Olsson, 1868.
Distoma (*Dicrocoelium*) *furcigerum* (Olsson) Stossich, 1886.
Leioderma furcigerum (Olsson) Stafford, 1904.
Fellodistomum furcigerum (Olsson) Yamaguti, 1953.

TYPE-HOST AND LOCALITY. *Limanda limanda*, Varberg, Sweden.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas denticulatus [intestine] Iceland–Faroes channel (64°N, 10°W; depth 592–620 m; June, 1974). BM(NH) 1977.3.2.3–8.

Glyptocephalus cynoglossus [intestine] Gothenburg, Sweden (Sept. 1973). Material of J. Thulin.

—— [intestine] Moray Firth, Scotland (58°N, 02°W; depth 89–140 m; July, 1976). BM(NH) 1977.3.2.1.

Hippoglossoides platessoides [intestine] Aberdeen, Scotland (Oct., 73). BM(NH) 1978.1.30.1–4.

—— [intestine] Shetland Isles, Scotland (60°N, 01°E; depth 136–144 m; July, 1976). BM(NH) 1977.3.2.2.

Limanda limanda [intestine] Cullercoats, Northumberland, England (May, 1972). Material of J. Thulin.

Lycenchelys sarsi [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

Lycodes esmarki [intestine] Foula, off NW Scotland (60°N, 06°W; depth 1000–1020 m; June, 1974). BM(NH) 1977. 3.2.9–12.

Lycodes vahli [intestine] Mid-Skagerrak, between Denmark and Sweden (Dec., 1970). Material of J. Thulin.

—— [intestine] Tjärnö, Sweden (June, 1971) Material of J Thulin.

Lycodes sp. [intestine] Iceland–Faroes channel (64°N, 10°W; depth 720–748 m; June, 1974). BM(NH) 1977.3.2.13–15.

Microstomus kitt [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

Reinhardtius hippoglossoides [intestine] NNE of Rona, Scotland (60°N, 05°W; depth 770–800 m; April, 1973). BM(NH) 1977.3.2.16.

—— [intestine] Anton Dohrn Bank, East Greenland (66°N, 30°W; depth 380–390 m; May, 1973). BM(NH) 1977.3.2.17.

—— [intestine] Iceland–Faroes channel (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) 1977.3.2.18.

(b) From elsewhere

Anarhichas minor [intestine] Newfoundland (see Bray, 1979 : 419). BM(NH) 1977.2.16.1.

Glyptocephalus cynoglossus [intestine] Newfoundland, Labrador and Nova Scotia (see Bray, 1979 : 419). BM(NH) 1977.2.16.2–12.

Hippoglossoides platessoides [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.13–50.
Limanda ferruginea [intestine] Nova Scotia (see Bray, 1979 : 420). BM(NH) 1977.2.16.51–52.
Myoxocephalus octodecemspinosus [intestine] Nova Scotia (see Bray, 1979 : 420). BM(NH) 1977.2.16.53.
Urophycis tenuis [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.54.

(ii) NE Atlantic records from the literature
[?] *Gadus morhua* [pylorus] Locality not given. McLaren & Hockley (1977 : 147) [this would appear to be a questionable record].
Glyptocephalus cynoglossus [intestine] Northumberland, England. Lebour (1908*a* : 33).
—— [intestine] Aberdeen, Scotland. Nicoll (1913 : 190).
Gymnacanthus tricuspis [intestine] East Greenland. Odhner (1905 : 305).
Hippoglossoides platessoides [stomach & intestine] Varberg (Aug.) and Øresund (May), Sweden. Olsson (1868 : 26; as *Distoma furcigerum*).
—— [intestine] Northumberland, England. Lebour (1908*a* : 33).
—— [intestine] Aberdeen, Scotland. Nicoll (1913 : 190).
—— [intestine] Øresund. Køie (1979: 127).
Limanda limanda [stomach & intestine] Varberg, Sweden (July, Aug.). Olsson (1868 : 26; as *Distoma furcigerum*).
—— [intestine] West coast of Sweden. Odhner (1905 : 305).
—— [stomach & intestine] St Andrews, Fife, Scotland. Nicoll (1907 : 72).
—— [intestine] Northumberland, England. Lebour (1908*a* : 33).
—— [intestine] Millport, Firth of Clyde, Scotland. Nicoll (1910 : 347; as *Leioderma furcigerum*).
—— [intestine] Aberdeen, Scotland. Nicoll (1915*a* : 360).
—— [intestine] Galway, Ireland. Little (1929 : 26, 27).
—— [intestine] Øresund. Køie (1979: 127).
Lophius piscatorius [intestine] Northumberland, England. Lebour (1908*a* : 33 – probably a 'fortuitous' host – Nicoll, 1909*b* : 16).
Lycodes pallidus [intestine] East Greenland. Odhner (1905 : 305).
Microstomus kitt [intestine] Northumberland, England. Lebour (1908*a* : 33).
Pleuronectes platessa [intestine] Northumberland, England. Lebour (1908*a* : 33).
—— [intestine] Øresund. Køie (1979: 127).

ASPECTS OF BIOLOGY. Records of intermediate hosts in the NE Atlantic.
(a) Intermediate hosts
Nuculana minuta [?] Øresund. Køie (1979: 124).
(b) (?) Accidental invertebrate host.
Buccinum undatum [stomach & oesophageal caecum] Øresund. Køie (1969 : 266).
Neptunea antiqua [?] Øresund. Køie (1979: 126).

Chubrik (1966) stated that the sporocysts and cercariae occur in the bivalve *Nuculana pernula* in the Barents Sea region and Køie (1979) found *N. minuta* infested in Øresund and west Greenland. The large, cylindrical daughter-sporocysts contain 30–70 developing cercariae, which differ from those reckoned to be *Fellodistomum fellis* in that they lack furcae on the long, narrow tail and have a distinctly 'Y'-shaped excretory vesicle. Køie (1969) and Yamaguti (1975) point out that the metacercaria is not known, although the encysted worms found by Nicoll & Small (1909) (see p. 206) may belong to this genus. Køie (1969) has repeatedly found immature *S. furciger* in the common whelk *Buccinum undatum* in Øresund between Denmark and Sweden, but never at Kristineberg or Gullmarfjord to the north. Although the same size as those from fish, they were rarely found with fully-developed eggs. Køie considered that the whelk is an accidental host. She points out that the whelk has roughly the same diet as the flatfishes which are the most common hosts of this parasite. Scott (1975*a*) found no clues as to the identity of the second intermediate host when he discovered that there was no obvious relationships between incidence and fish-length in infestations of *Hippoglossoides platessoides* in the north-west Atlantic.

Recently, Køie (1979) has shown that, in fact, the metacercarial stage is omitted, the final host feeding directly on the cercaria.

Levinsen's (1881) description and our own observations indicate that spermatophores may be formed by this worm.

Although flatfishes appear to be the most frequent hosts of this parasite, it also occurs in a variety of other fishes, especially eelpouts. It has a circumpolar distribution, having been found across northernmost regions of the Atlantic and Pacific Oceans, as well as in the Barents, White and Kara Seas. Although reaching as far south as Massachusetts in the western North Atlantic (Linton, 1940) and Britain and Ireland in the east, its main area of distribution is probably in the sub-arctic and arctic seas. In the Pacific its known southern limits are Japan in the west (Yamaguti, 1934) and Washington State in the east (Ching, 1960). We have examined the specimens recorded from the English Channel at Plymouth by Baylis & Jones (1933) and Baylis (1939), and we consider them to be immature specimens of *Steringotrema pagelli* (van Beneden, 1871).

In the waters off the eastern coast of Canada this parasite may be a biological indicator ('tag') for stocks of the long rough dab *Hippoglossoides platessoides*. Scott (1975*b*) found a high incidence in the Gulf of St Lawrence and a lower incidence in other Canadian fishing grounds, and he pointed out that this supports other evidence that the Gulf of St Lawrence stock is distinct.

PREVIOUS DESCRIPTIONS. Olsson (1868 : 28; as *Distoma furcigerum*); Levinsen (1881 : 61; as *Distomum furcigerum*); Odhner (1905 : 305); Lebour (1908*a* : 33); Yamaguti (1934 : 405); Linton (1940 : 39); Miller (1941 : 44); Polyansky (1955 : 52); Strelkov (1960 : 156).

DESCRIPTION (Fig. 3). This description is based upon 92 whole-mounted and 6 serially sectioned specimens. These worms have an elongate oval body-shape, being more or less fusiform in young specimens (Fig. 3b) and possessing an elongate, parallel-sided hindbody in older worms (Fig. 3a). The body-surface is smooth. The dimensions of the worms are summarized in Table 2.

The subterminal, globular *oral sucker* is smaller than the slightly transversely elongate-oval *ventral sucker*, the ratio being 1 : 1·5–2·3. In young specimens the ventral sucker is situated at about one-third of the body-length from the anterior end, but in older specimens it becomes more anteriorly situated as the hindbody grows allometrically. The parenchymal cells of the body of this worm envelop numerous patches of glandular cells, which also occur embedded less densely in the musculature of the suckers. There is a small prepharynx which leads into a subglobular *pharynx*, and this in turn leads into an oesophagus that is usually about the same length or a little longer than the pharynx. The intestinal bifurcation occurs at the level of the genital pore, and two narrow caeca pass back beyond the testes, but terminate prior to reaching the middle of the post-testicular zone.

The terminal *excretory pore* leads into a 'Y'-shaped vesicle, the stem of which reaches forward to the testes before bifurcating. The arms of the vesicle pass between the testes, then dorso-laterally to the ventral sucker and into the forebody as far as the pharynx.

The *testes* lie in the anterior half of the hindbody in a more or less symmetrical arrangement. Their margins are smooth or slightly indented. The narrow vasa efferentia enter the cirrus-sac separately, but close together. The *cirrus-sac* is a large, oval structure lying just anteriorly to the ventral sucker and overlapping it to a small extent. It contains a bipartite seminal vesicle of variable size, the proximal part of which is often smaller and contains less sperm than the distal part (Fig. 3d), but both parts may be empty and therefore narrow (Fig. 3c). The wide pars prostatica is similar to that of *Fellodistomum fellis* in shape and in the nature of the lining and the wide, irregular ejaculatory duct is also similar. The genital atrium is quite small compared with the ejaculatory duct and opens, via the genital pore, just posterior to the middle of the forebody to the left of the median line.

Immediately antero-dextral to the right testis lies the multilobate *ovary*. The oviduct arises posteriorly and receives Laurer's canal and a narrow common vitelline duct before entering a large Mehlis' gland, which lies directly posterior to the ovary. Laurer's canal is short and opens dorsally at the level of the posterior margin of the ovary. The *uterus* passes anteriorly from Mehlis' gland,

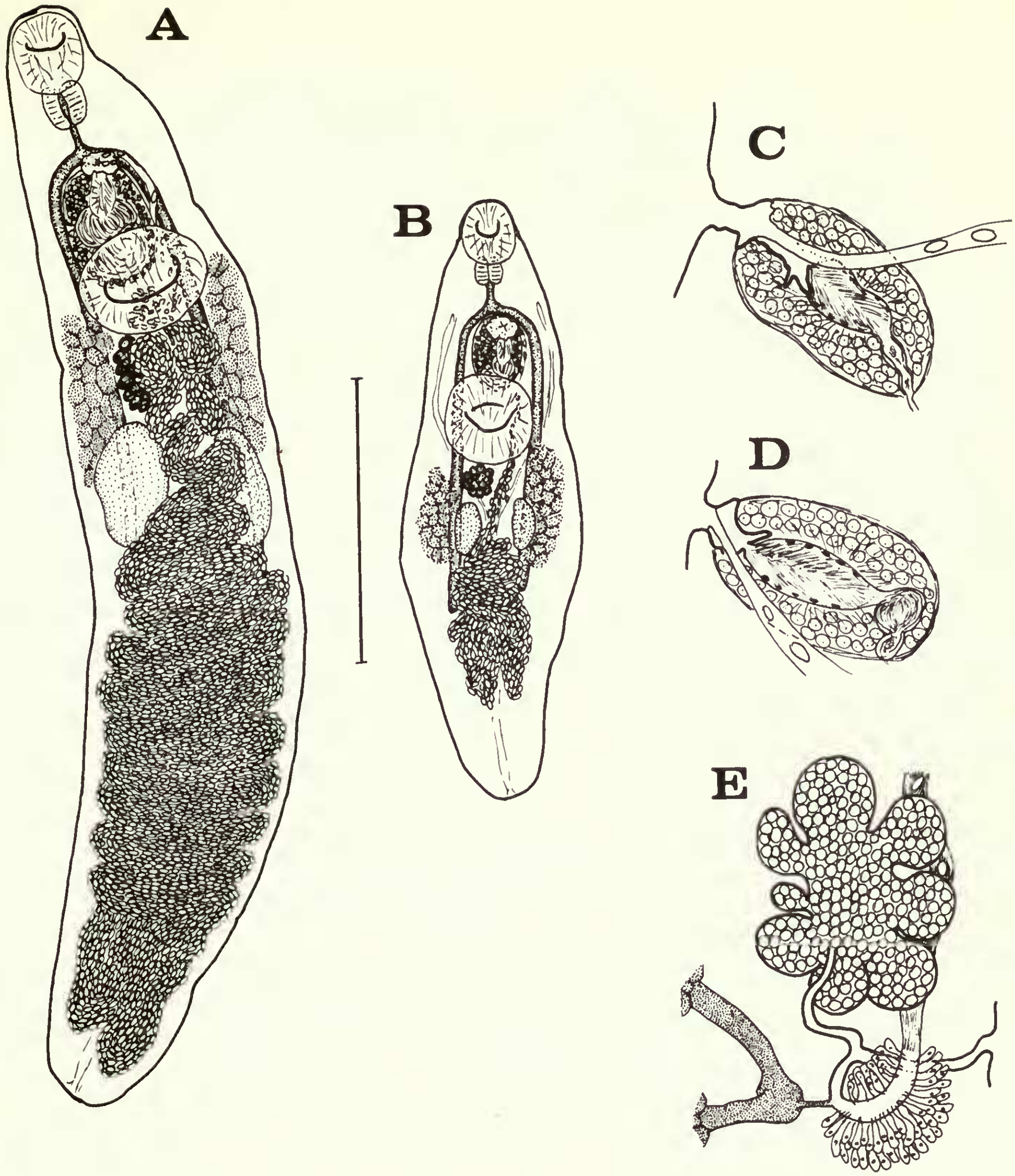

Fig. 3 *Steringophorus furciger*: (a) large specimen from *Reinhardtius hippoglossoides*; (b) early mature specimen from *Hippoglossoides platessoides*; (c) cirrus-sac with almost empty seminal vesicle; (d) cirrus-sac with partly empty seminal vesicle; (e) diagram of female proximal genitalia. Bar scale: a, b = 1 mm.

and its initial loops constitute a uterine seminal receptacle (Fig. 3e). The bulk of the uterus, however, coils in the post-testicular region of the hindbody, but it appears that as the worm ages the part of the uterus between the testes and the ventral sucker also fills with eggs. The uterus passes dorsally to the ventral sucker as a straight, narrow duct and opens into the genital atrium laterally to the cirrus-sac. The numerous eggs have smooth shells, but they may possess a small boss on the anopercular pole. Many worms have some small, deformed eggs; but, with the exception of one specimen from *Lycenchelys sarsi*, all contain some full-sized eggs. The vitelline follicles lie in two

Table 2 Dimensions of *Steringophorus furciger* from the present material and from the literature

Authority	Odhner (1905)	Lebour (1908*a*)	Yamaguti (1934)	Strelkov (1960)	Present material
Hosts	*Gymnacanthus ventralis* *Lycodes pallidus* +Olsson's	Flatfish (5 spp.) *Lophius piscatorius*	*Bothrocara zesta* *Furcimanus nakamurae*	Flatfish (4 spp.) *Theragra chalcogramma*	see text
Locality	E. Greenland, etc.	Northumberland	Japan	E. Kamchatka	see text
Length (mm)	3·5	1·5–3·5	1·87–3·12	2·1–5·0	1·35–4·08
Breadth (mm)	0·6–1·1	–	0·85–1·18	0·8–1·4	0·62–1·16
Length : forebody ratio	(1 : 0·22)	(1 : 0·30)	–	–	1 : 0·18–0·44
Oral sucker (mm)	0·2–0·3	0·2	0·20–0·28 × 0·20–0·32	0·24–0·31	0·14–0·33 × 0·17–0·34
Ventral sucker (mm)	0·35–0·55	0·35	0·28–0·46 × 0·36–0·60	0·49–0·60	0·24–0·56 × 0·23–0·54
Sucker-ratio	1 : 1·7	1 : 1·7	–	–	1 : 1·5–2·3
Pharynx (mm)	–	–	0·10–0·13 × 0·10–0·12	0·14–0·19 × 0·10–0·14	0·10–0·17 × 0·07–0·17
Oesophagus (mm)	0·10–0·13	–	0·05–0·15	–	0·04–0·33
Cirrus-sac (mm)	–	–	0·47–0·32	–	0·17–0·45 × 0·10–0·33
Testes (mm)	–	–	0·25–0·46 × 0·21–0·36	0·27–0·37	0·15–0·37 × 0·11–0·55
Ovary (mm)	–	–	–	0·18–0·30	0·15–0·28 × 0·12–0·38
Eggs (μm)	46–66 × ?	46 × 19	60–68 × 34–36	45–54 × 16–24	42–54 × 23–33

tightly packed lateral fields reaching from the level of the hinder margin of the ventral sucker to a level between the anterior margin of the testes and immediately posterior to the testes. The main vitelline collecting ducts unite ventrally to Mehlis' gland to form a small reservoir which is connected to the oviduct via a short, narrow common duct.

DISCUSSION. There are one or two features of this worm on which there is disagreement in the literature. Levinsen (1881) and Lebour (1908*a*) claim to have seen a distinct seminal receptacle; but we have been unable to trace one in our specimens. We tend to agree with Odhner (1905), who suggested that Levinsen in fact saw just a small inflation of Laurer's canal, possibly a structure which we (Gibson & Bray, 1979) refer to as a 'rudimentary seminal receptacle'. Although we have not seen such a dilation, Lebour (1908*a*) stated that Laurer's canal led from the seminal receptacle (this is clearly shown in her Fig. 7), and Yamaguti (1934) says, 'there is a small receptaculum seminis which may be considered a dilatation of the [*sic*] Laurer's canal'. Linton (1940) also failed to find any structure, other than the uterine seminal receptacle, which acted as a sperm-store in the female part of the reproductive system.

Yamaguti (1934) and Miller (1941) consider that the genital pore is normally medially situated; but Odhner (1905) stated that this is abnormal, and in most of our material the genital pore lies to the left of the median line.

A suspicion that all of the records may not be of the same species is aroused by the reports of egg-sizes well above those found in our specimens and in the majority of specimens described in the literature. Odhner (1905) found that his specimens from *Lycodes pallidus* and *Gymnacanthus tricuspis* had eggs between 60 and 66 μm in length, and Yamaguti's (1934) specimens had eggs of 60 to 68 μm in length. A close examination of further specimens with these large eggs is desirable. Our own specimens from *Lycodes esmarki*, *L. vahli* and *Lycodes* sp. all had eggs between 42 and 50 μm in length.

Steringophorus agnotus (Nicoll, 1909) Dollfus, 1952

Fellodistomum agnotum Nicoll 1909.
Fellodistomum incisum (Rudolphi) of Stafford (1904) in part (?).

TYPE-HOST AND LOCALITY. *Anarhichas lupus*, St Andrews, Fife, Scotland.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Anarhichas lupus [bile-duct] Eldey Bank, off Reykjanes, Iceland (64°N, 24°W; depth 148–152 m; May, 1974). BM(NH) 1977.3.4.1–2.

—— [bile-duct] Moray Firth, Scotland (58°N, 02°W; depth 164 m; July, 1976). BM(NH) 1977.3.4.3.

(b) From elsewhere

Anarhichas lupus [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.55.

(ii) NE Atlantic records from the literature

Anarhichas lupus [gall-bladder & duodenum] St Andrews, Fife, Scotland. Nicoll (1909*a* : 469; as *Fellodistomum agnotum*).

—— [anterior intestine] Trondheim, Norway. Odhner (1911*a* : 99).

—— [bile-duct] Húsavík, Neskaupstadur and Reykjavik, Iceland. Brinkmann (1956 : 22; as *Fellodistomum agnotum*).

Anarhichas minor [gall-bladder] Umîvik, East Greenland. Brinkmann (1975 : 52; as *Fellodistomum agnotum*).

ASPECTS OF BIOLOGY. This parasite is found in anarhichadid fishes in the North Atlantic Ocean and the Barents Sea. It has been confused in the past with *Fellodistomum fellis* (see Dawes, 1947) which occurs in the same host; but it apparently has a slightly different site-preference. While *F. fellis* occurs almost exclusively in the gall-bladder, *S. agnotus* apparently occurs in the duodenum (Polyansky, 1955 : 56), as well as in the bile-duct and gall-bladder. The largest specimen that we found came from the intestine, but our other eight specimens all came from the bile-duct.

The life-history of this species is unknown.

PREVIOUS DESCRIPTIONS Nicoll (1909*a* : 469; as *Fellodistomum agnotum*); Miller (1941 : 43; as *F. agnotum*); Polyansky (1955 : 56; as *F. agnotum*); Brinkmann (1956 : 22; as *F. agnotum*); Srivastava & Ghosh (1968 : 49; as *F. agnotum*).

DESCRIPTION (Fig. 4). Eight whole-mounts and one sectioned specimen were studied. These worms are less robust than *Fellodistomum fellis* (see Table 3 for dimensions). The body is widest at the level of the ventral sucker, the forebody tapering sharply and the hindbody, which in some cases is quite extensive, narrowing more slowly (Fig. 4a & b). The body-surface bears no spines and the body-wall is thin. The subterminal, globular *oral sucker* is smaller than the more or less globular *ventral sucker*, which is situated at about one-third of the body-length from the anterior extremity. The sucker-ratio is 1 : 1·3–1·7. There is a short prepharynx, visible only in sections, which leads into a globular to elongate-oval *pharynx* just less than half of the diameter of the oral sucker. The pharynx leads directly into two wide caeca, which terminate just posteriorly to the testes, although not always symmetrically. The semi-digested remains of blood can often be seen in the lumen of the caeca.

At the posterior extremity the 'Y'-shaped *excretory vesicle* opens via the excretory pore. The vesicle, which lies dorsally to the gonads but ventrally to the caeca, bifurcates at about the level of the right testis. The arms reach almost to the level of the pharynx, becoming more dilate in the forebody.

The oval to elongate-oval *testes* lie obliquely with their longitudinal axes oriented antero-posteriorly. The left testis lies more anteriorly than the right, although in our smallest immature specimen the testes are more or less symmetrical. The vasa efferentia pass through the wall of the

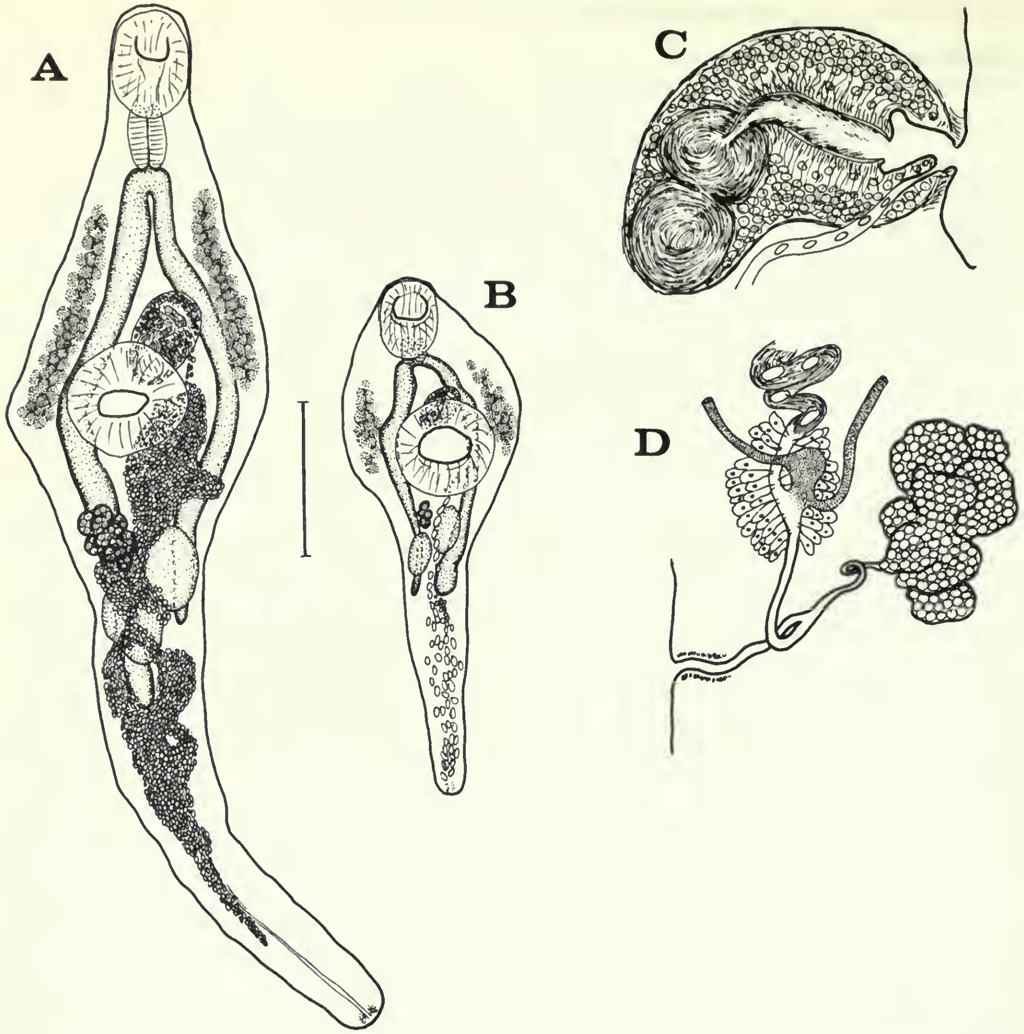

Fig. 4 *Steringophorus agnotus*: (a) specimen from intestine, with small, malformed eggs; (b) small specimen from bile-duct; (c) cirrus-sac; (d) diagram of female proximal genitalia. Bar scale: a, b = 0·5 mm.

cirrus-sac separately, but close together. The *cirrus-sac*, which is present close to the anterior margin of the ventral sucker (Fig. 4c), has a thin muscular wall. It lies at an angle to the body-surface, causing difficulties in accurate measurement in whole-mounts, and contains a bipartite seminal vesicle, a wide pars prostatica surrounded by numerous gland-cells, and a wide ejaculatory duct. The structure of the cirrus-sac and its contents is similar to that of the previous two species, particularly in the filamentous lining of the pars prostatica and the muscular, diverticulate nature of the ejaculatory duct. The genital atrium is small, receiving the female duct from the left side laterally to the cirrus-sac. The genital pore is large, surrounded by an almost sucker-like musculature, and situated to the left of the median line just anteriorly to the ventral sucker.

The multilobate *ovary* lies almost immediately anterior to the right testis. A narrow oviduct passes from its dorsal surface and runs posteriorly to where it unites with Laurer's canal and the common vitelline duct prior to entering Mehlis' gland. In fact the union with the broad common vitelline duct occurs just as the oviduct enters Mehlis' gland. Laurer's canal opens to the exterior at a level just posterior to the ovary (Fig. 4d). There is no seminal receptacle associated with Laurer's canal; but the first few coils of the *uterus* form a uterine seminal receptacle. The uterus is initially coiled just anteriorly to Mehlis' gland, and then coils posteriorly between the testes, reaching close to the posterior extremity. On returning forward it forms a number of coils at the level of the posterior margin of the ventral sucker, before passing anteriorly towards the genital atrium. The terminal region of the uterus which unites with the genital atrium is narrow. The uterus contains numerous 'normal' eggs and often many smaller, apparently malformed, eggs and fragments of vitelline material. The vitelline follicles lie in two lateral fields, reaching from about the level of the middle of the ventral sucker to a level just posterior to the pharynx.

Table 3 Dimensions of *Steringophorus agnotus* from the present material and from the literature

Authority	Nicoll (1909*a*)	Miller (1941)	Srivastava & Ghosh (1968)	Present material
Hosts	*Anarhichas lupus*	*Anarhichas lupus*	*Lophius piscatorius*	*Anarhichas lupus*
Locality	Scotland	Canada	unknown	see text
Length (mm)	up to 3·3	2·9	2·95	1·3–3·4
Breadth (mm)	up to 0·87	1·09	1·25	0·43–0·82
Length : forebody ratio	(1 : 0·36)	(1 : 0·35)	(1 : 0·36)	1 : 0·26–0·41
Oral sucker (mm)	0·34 (in 3 mm specimen)	0·29 dia.	0·31 × 0·36	0·20–0·36 × 0·18–0·26
Ventral sucker (mm)	0·51 (in 3 mm specimen)	0·42	0·45 × 0·49	0·29–0·40 × 0·28–0·41
Sucker-ratio	1 : 1·5	(1 : 1·4)	1 : 1·46	1 : 1·3–1·7
Pharynx (mm)	0·15 × 0·12	0·14 long	0·14 × 0·13	0·097–0·13 × 0·090–0·25
Cirrus-sac (mm)	–	–	–	0·28–0·32 × 0·19–0·22
Testes (mm)	–	–	0·18–0·24 × 0·13–0·20	0·18–0·30 × 0·07–0·17
Ovary (mm)	–	–	0·27 × 0·13	0·13–0·19 × 0·05–0·18
Eggs (μm)	48 × 24	44 × 24	45 × 27	52–61 × 25–29 (+ many malformed)

DISCUSSION. This species exhibits features which are intermediate between *Fellodistomum fellis* and *Steringophorus furciger* both in morphology and biology. It was moved from *Fellodistomum* to *Steringophorus* by Dollfus (1952), on the basis of the extension of the uterus into the post-testicular region, and although it does not appear to have been accepted by any subsequent worker we agree with this move. We have not, however, followed Dollfus in distinguishing these two genera at the subfamily level, as *S. agnotus* is similar to *F. fellis*.

Dawes (1947) considered *Fellodistomum agnotum* to be a synonym of *F. fellis*, but detailed and convincing rebuttals of this have been presented by Polyansky (1955), who lists five distinguishing features, and Brinkmann (1956), who lists ten. Dawes stated, '. . . it is very difficult to conceive of the existence of two distinct species of such rarity and precise host-specificity'. Subsequent work has shown that these species are neither as rare nor as host-specific as Dawes apparently considered them (Brinkmann, 1975). As mentioned above, Yamaguti (1971) regarded *Fellodistomum* as a young form of *Steringophorus* because of the restricted distribution of the uterus in the former, which he suggested varies with age. The extension of the uterus into the post-testicular region of *S. agnotus*, however, is not a sign of maturity, as even the smallest worms have primordia of the uterus in this region.

We have found that in all of our specimens the caeca extend just posteriorly to the testes. Nicoll (1909*a*) and Miller (1941) describe the caeca as reaching the testes, but not going beyond, and in the specimen figured by Srivastava & Ghosh (1968) the caeca did not reach the testes. The latter figure is of a worm which is obviously considerably flattened, and this procedure has probably affected the relative positions of these organs, as is suggested by the median position of the genital pore. It would seem likely that Nicoll's and Miller's (i.e. Stafford's) material may also have been fixed under pressure. Our material was all fixed without pressure in glacial acetic acid. The two specimens studied by Srivastava & Ghosh (1968) were found amongst the slide collection of the late Dr G. S. Thaper and are purported to have been recorded from the gall-bladder of *Lophius piscatorius* from an unknown locality. When the distribution of this host and of the usual host is taken into consideration, it would seem likely that this material came from European or at least northern Atlantic waters. These specimens also differ from other descriptions of *S. agnotus* in appearing to possess a short oesophagus. Brinkmann (1956) uses egg-length as a criterion distinguishing *F. fellis* ('45 μm') and *S. agnotus* ('55 μm'). As Table 3 indicates, this may well be an unsatisfactory character in that some authors have recorded an egg-length in *S. agnotus* similar to that in *F. fellis*. We found that careful examination of eggs lying horizontally *in situ* gave measurements of 52–61 μm. It is most noticeable, however, that many eggs, and in fact all of them in the specimen recovered from the intestine (Fig. 4a), are apparently malformed and much smaller than usual (25–29 μm). The worms from the bile-duct have either a mixture of large and small eggs or large eggs only.

Steringophorus blackeri Bray, 1973

TYPE-HOST AND LOCALITY. *Xenodermichthys socialis* [=*copei*], Bay of Biscay (45°N, 02°W).

RECORDS

(i) Material studied

(a) From the NE Atlantic

Xenodermichthys socialis [intestine & body-cavity] Bay of Biscay (45°N, 02°W; depth 575–665 m; Jan., 1971). Type-material (see Bray, 1973 : 174). BM(NH) 1973.4.9.21–24.

—— [intestine] Porcupine Bank, W. of Ireland (54°N, 14°W; depth 1000 m; June, 1974). BM(NH) 1977.3.15.1.

—— [body-cavity] Rosemary Bank, NW of Scotland (59°N, 10°W; depth 970–1025 m; June, 1974). BM(NH) 1977.3.15.2.

—— [intestine] Flannan region, NW of Scotland (59°N, 09°W; depth 900–940 m; Oct., 1978). BM(NH) 1979.2.14.1.

(b) From elsewhere

Xenodermichthys sp. [intestine] Off Moroccan coast (28°N, 14°W; depth 390 m) (see Bray, 1973 : 174). BM(NH) 1973.5.17.4–5.

(ii) NE Atlantic records from the literature

Xenodermichthys socialis [intestine & body-cavity] Bay of Biscay. Bray (1973 : 174).

ASPECTS OF BIOLOGY. All of the records of this parasite are given above, thus indicating that it has only been found in the alepocephalid genus *Xenodermichthys* from the eastern North Atlantic. The worms are rather large in comparison with the lumen of the intestine, where they normally reside. In many cases they appear to quite effectively block the gut, and, as the wall of the intestine surrounding them is severely stretched, it is easy to imagine them breaking through into the body-cavity, where a number have been found.

PREVIOUS DESCRIPTION. Bray (1973 : 174).

DESCRIPTION (Fig. 5). Thirteen whole-mounted and two sectioned specimens were available for study, the measurements of which are given in Table 4. The shape of the body of these large worms may be broadly oval, especially in specimens from the body-cavity, to elongate-oval,

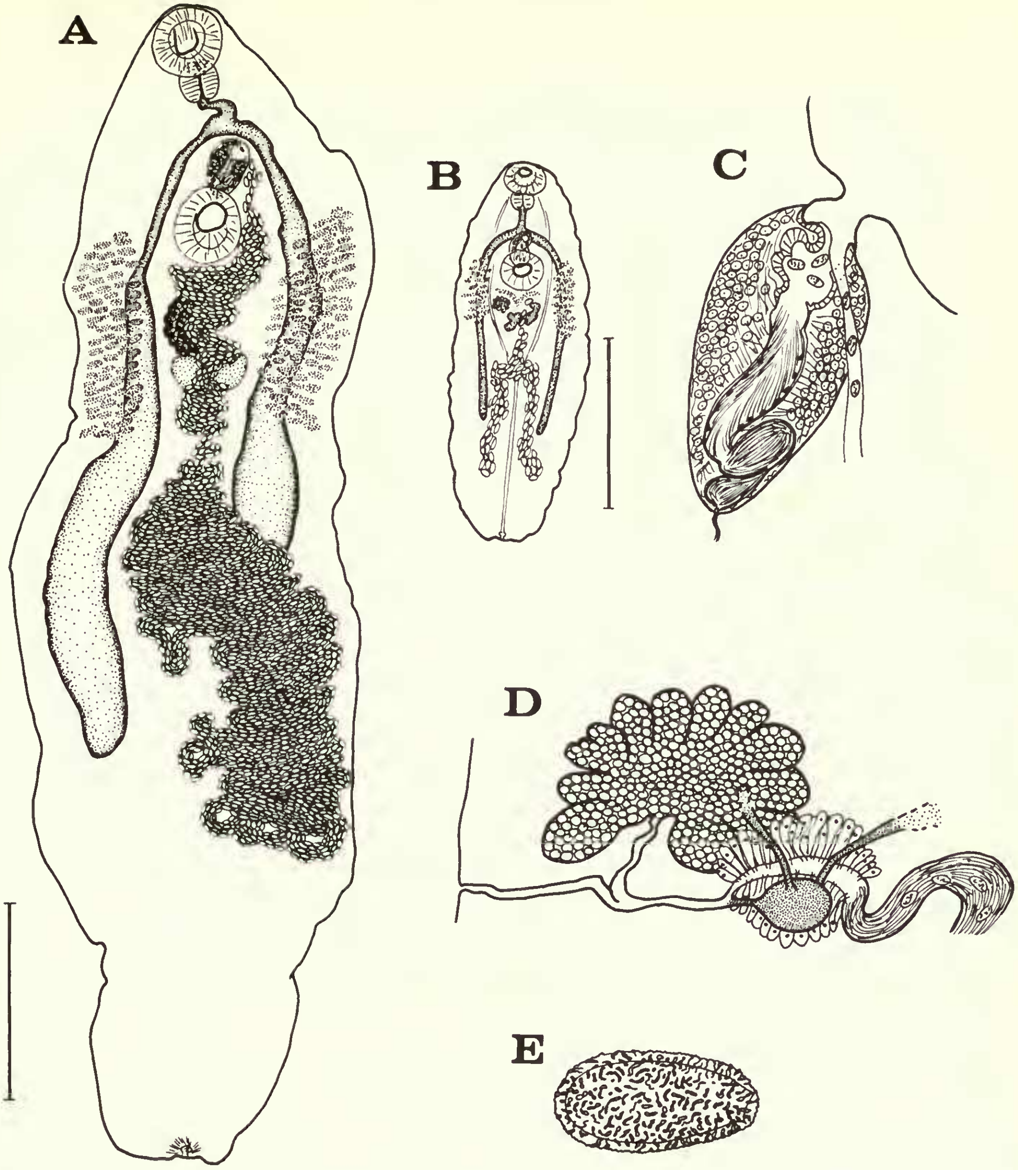

Fig. 5 *Steringophorus blackeri*: (a) large specimen from intestine; (b) small specimen from intestine; (c) cirrus-sac; (d) diagram of female proximal genitalia; (e) egg. Bar scales: a, b = 1 mm.

especially in large specimens from the intestine (Fig. 5a). One specimen is divided into three more or less equal parts by two constrictions, which thus give it a moniliform appearance. The forebody is smaller than the hindbody in the ratio of 1 : 3–6; but with this ratio increasing allometrically with increased length of the worms. The body-surface is smooth. There is a globular, subterminal *oral sucker*, which is similar in size to, but may be slightly smaller or larger than, the globular *ventral sucker*. There is a short prepharynx, a large *pharynx* and a short oesophagus which is surrounded by gland-cells. The intestinal bifurcation, which occurs at about the middle of the forebody, gives rise to caeca which reach posteriorly to about the middle of the hindbody, normally terminating amongst the coils of the uterus. These caeca may be narrow or wide, and are often full of the semi-digested remains of blood.

Table 4 Dimensions of *Steringophorus blackeri* from the present material and from the literature

Authority	Bray (1973)	Present material (collected 1974 & 1978)
Length (mm)	2·2–9·0	3·0–5·95
Breadth (mm)	0·8–2·04	1·20–2·1
Length : forebody ratio	1 : 0·14–0·29*	1 : 0·15–0·27
Oral sucker (mm)	0·24–0·47 dia.	0·30–0·40 × 0·27–0·43
Ventral sucker (mm)	0·24–0·49 dia.	0·27–0·42 × 0·30–0·50
Sucker-ratio	1 : 0·85–1·12	1 : 0·84–1·24
Pharynx (mm)	0·11–0·26 × 0·125–0·32	0·21–0·26 × 0·20–0·26
Oesophagus (mm)	0·105–0·23	0·09–0·17
Cirrus sac (mm)	0·21–0·35 × 0·12–0·19	0·25–0·35 × 0·16–0·23
Testes (mm)	0·07–0·21 × 0·14–0·20	0·20–0·27 × 0·11–0·21
Ovary (mm)	0·18–0·27 × 0·11–0·27	0·18 × 0·13
Eggs (μm)	52–63 × 27–34	48–54 × 26–34

* New data.

The *excretory pore* is terminal and leads into a 'Y'-shaped vesicle, the stem of which may be narrow, especially in specimens from the intestine, or wide and dilate, especially in specimens from the body-cavity. Just posterior to the gonads the vesicle bifurcates, and the arms, which are usually narrow, reach into the forebody to the level of the pharynx.

In young specimens the small, oval *testes* have quite deeply indented margins, but in the larger specimens they are entire. They occur close to each other, almost symmetrically or obliquely with the left testis the more anterior, in the anterior quarter of the hindbody. The vasa efferentia are difficult to follow, but appear to remain separate until after they have passed through the wall of the cirrus-sac. The *cirrus-sac* is oval and tapers slightly at the proximal end (Fig. 5c). It contains a small, bipartite seminal vesicle, a wide, curved pars prostatica with a filamentous lining and a wide, diverticulate ejaculatory duct which may contain eggs. The cirrus-sac and contents are, therefore, typical of this subfamily. The genital atrium is small, receiving the metraterm laterally to the cirrus-sac, and opens via the genital pore just to the left of the median line in the hinder region of the forebody.

Immediately anterior to the right testis lies a multilobate *ovary*. The oviduct leaves this posteriorly and receives Laurer's canal and the common vitelline duct prior to passing into Mehlis' gland (Fig. 5d). Laurer's canal opens dorsally at the level of Mehlis' gland, and often contains small amounts of spermatozoa. A uterine seminal receptacle is the only seminal store in the female part of the reproductive system. Most of the *uterus* lies posteriorly to the gonads: it passes back medially with laterally directed loops to about the middle of the worm, and then descends in a series of loops on one, or more usually on both, sides of the body to about two-thirds of the way down the hindbody. The post-testicular region of the uterus, therefore, often possesses the outline of an inverted 'Y' (Fig. 5b). Anterior to the gonads the uterus tends to pass forward directly to the genital atrium in young specimens, but in the largest specimens it often coils in the region between the gonads and the ventral sucker. There is always a considerable portion of the posterior hindbody devoid of uterine coils. The operculate eggs are variable in size, and the brownish-yellow shells bear a pattern of raised bosses (Fig. 5e). The *vitellarium* consists of two lateral fields of globular or short, transversely-elongate follicles, lying between the anterior margin of the ventral sucker and a level just posterior to the testes. The two fields feed main vitelline ducts which pass medially ventral to Mehlis' gland and unite to form a common vitelline duct. This common duct is dilate proximally, forming a distinct vitelline reservoir.

DISCUSSION. This description extends that of Bray (1973), especially with regard to details of the cirrus-sac, which are corrected here, and the increased range of egg-sizes recorded. With regard to the sucker-ratio, about equal numbers of our specimens possessed a ventral sucker which was either slightly larger or smaller than the oral sucker. Another variable feature is the arrangement of uterine coils in the post-testicular region of the hindbody. The normal arrangement appears to be two lateral coils (Fig. 5b), but occasionally the uterus develops down one side of the body only (Fig. 5a). The difference in body-shape between specimens from the body-cavity and those from the intestine appears to be caused by differences in the dilation of the excretory vesicle. In specimens from the body-cavity the vesicle is wide, this possibly being caused by differences in the osmolarity of the two environments or by other factors, such as the health of the host, which might have upset the normal osmotic balance of these worms. The health of the fish may suffer when these worms pass through the gut-wall.

Steringophorus pritchardae (Campbell, 1975) n. comb.

Abyssotrema pritchardae Campbell, 1975.

TYPE-HOST AND LOCALITY. *Alepocephalus agassizi*, Hudson Canyon, NW Atlantic.

RECORDS
(i) Material studied
(a) From NE Atlantic

Alepocephalus bairdii [upper intestine] Porcupine Bank, W of Ireland (54°N, 14°W; depth 1000–1050 m; June, 1974). BM(NH) 1977.5.23.1–4.

—— [upper intestine] South Rockall, W of Scotland (55°N, 17°W; depth 821–850 m; June, 1974). BM(NH) 1977.5.23.5–6.

—— [upper intestine] Rosemary Bank, NW of Scotland (59°N, 10°W; depth 680–760 m; June, 1974). BM(NH) 1977.5.23.7–8.

—— [pyloric caeca] Sula Sgeir, NW of Scotland (60°N, 07°W; depth 900 m; June, 1974). BM(NH) 1977.5.23.9.

—— [intestine] Sula Sgeir region, NW of Scotland (59°N, 08°W; depth 1160–1220 m; Oct., 1978). BM(NH) 1979.2.14.2.

—— [intestine] Flannan region, NW of Scotland (59°N, 09°W; depth 1000 m; Oct., 1978). BM(NH) 1979.2.14.3.

(b) From elsewhere

Alepocephalus agassizi [intestine] Hudson Canyon, NW Atlantic (39°N, 71°W; depth 1919–2297 m (see Campbell, 1975 : 661).

(ii) NE Atlantic records from the literature
None

ASPECTS OF BIOLOGY. This species has been found only in *Alepocephalus* spp. in the NW and NE Atlantic in deep water down to nearly 2300 m. Campbell (1975) found 247 specimens in 20 *A. agassizi* with 100% incidence. This contrasts with the rate of infestation found in the NE Atlantic where the most found in any one specimen of *A. bairdii* was 6, and the rate of incidence was about 50%. On one occasion this species was found sympatric with *Olssonium turneri*. Spermatophores have been observed by Campbell (1975).

PREVIOUS DESCRIPTION. Campbell (1975 : 661; as *Abyssotrema pritchardae*).

DESCRIPTION (Fig. 6). This description is based on 25 specimens, two of which have been serially sectioned, from the NE Atlantic; and two whole-mounted and two sectioned specimens from the NW Atlantic. The worms are long, narrow, dorsoventrally flattened and bear a small protrusion at the posterior end of the body (Fig. 6a–c).

The dimensions of this species are summarized in Table 5. The body-surface is smooth, and the large *oral sucker* has a longitudinally elongate subterminal opening. It is slightly wider than the globular *ventral sucker*, which lies just inside the anterior quarter of the body. A short prepharynx leads into a small, globular *pharynx*, which, in turn, leads into a long oesophagus that extends back to about the level of the genital pore. At this point the gut bifurcates, giving rise to two

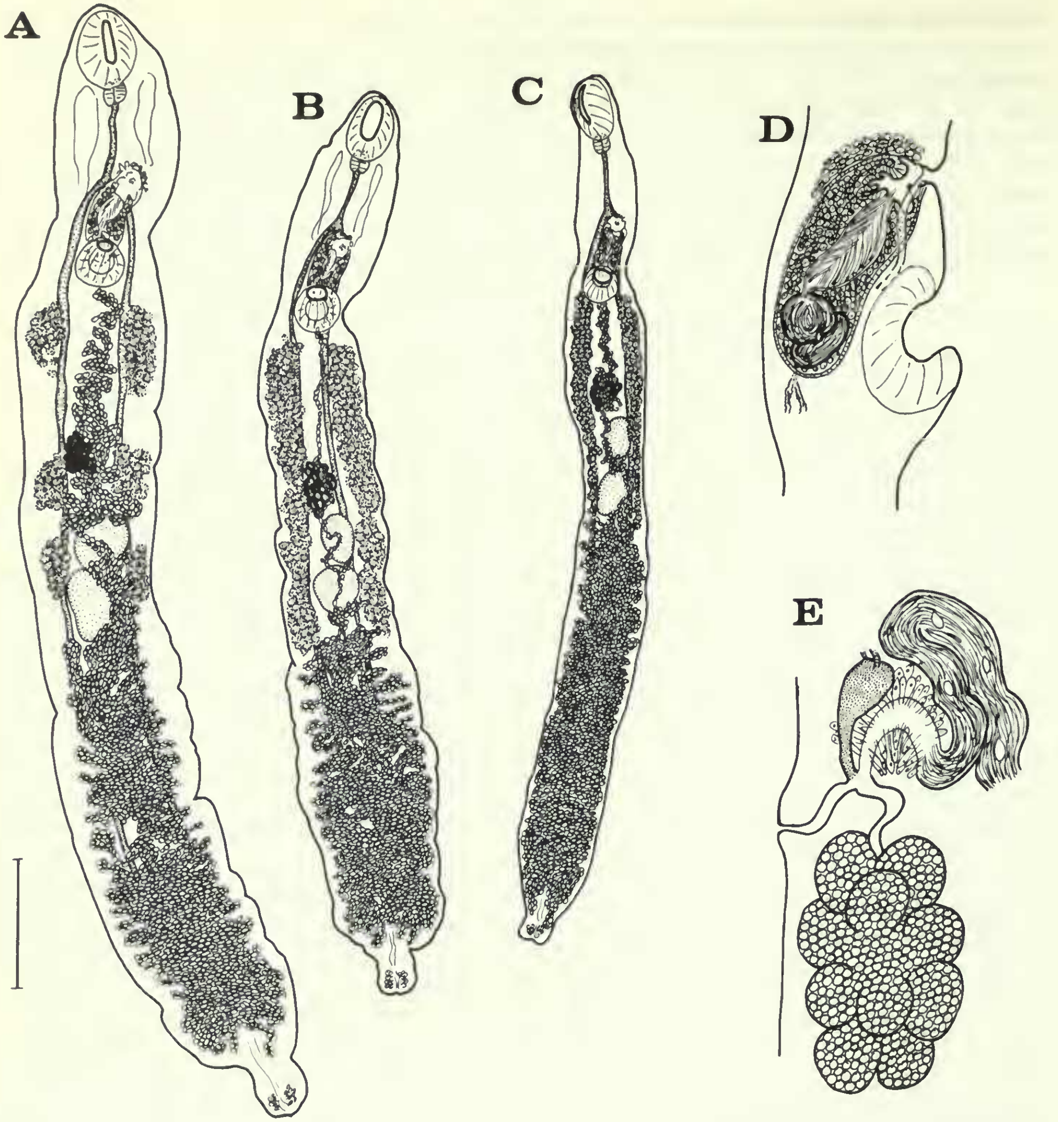

Fig. 6 *Steringophorus pritchardae*: (a–c) wholemount specimens, ventral view; (d) cirrus-sac; (e) diagram of female proximal genitalia. Bar scale: a–c = 1 mm.

narrow caeca which reach back to about the middle of the post-testicular region, where they end blindly.

The *excretory pore* lies at the posterior end of the body surmounted on a distinct protrusion. The initial part of the stem of the 'Y'-shaped vesicle is short, narrow, tubular and surrounded by numerous gland-cells. The main part of the stem is much wider and reaches forward to the level of the middle of the post-testicular region (approximately just anterior to the posterior limit of the gut-caeca), where it bifurcates and gives rise to two arms. These arms are quite wide and extend forward to about the level of the posterior margin of the oral sucker.

The two *testes* are oval, or irregularly oval, and lie in tandem in about the middle of the worm. The posterior testis is often slightly larger than the anterior testis. The vasa efferentia remain separate until close to the wall of the cirrus-sac; but it was not possible to ascertain whether or not they unite just outside it. The *cirrus-sac* is large, elongate-oval and its proximal region lies dorsal to the ventral sucker. It contains a bipartite seminal vesicle, either part of which may be the larger. The pars prostatica, which is surrounded by numerous gland-cells and has a filamentous lining, is wide and thus resembles that of other fellodistomines. The ejaculatory duct is also wide, but it is also muscular and distinctly pocketed. The genital atrium is small, and opens through the genital pore just to the left of the median line and just posterior to the middle of the forebody. Spermatophores may be present on the surface close to the genital pore. There is a sheath of gland-cells present lying across the anterior margin of the cirrus-sac (Fig. 6d).

Table 5 Dimensions of *Steringophorus pritchardae* from the present material and from the literature

Authority	Campbell (1975)	Present material
Host	*Alepocephalus agassizi*	*Alepocephalus bairdii*
Locality	NW Atlantic	NE Atlantic
Length (mm)	3·9–13·8	3·7–9·0
Breadth (mm)	1·1–3·8	0·44–1·2
Length : forebody ratio	(1 : 0·21)	1 : 0·17–0·27
Oral sucker (mm)	0·39–0·67 × 0·37–0·75	0·29–0·57 × 0·21–0·47
Ventral sucker (mm)	0·32–0·67 × 0·30–0·68	0·20–0·46 × 0·19–0·43
Sucker-ratio	1 : 0·85–0·94	1 : 0·91–0·94
Pharynx (mm)	0·21–0·34 dia.	0·08–0·19 dia.
Oesophagus (mm)	0·18–0·51	0·13–0·61
Cirrus-sac (mm)	0·62–1·2 × 0·32–0·55	0·30–0·78 × 0·13–0·25
Testes (mm)	0·37–0·69 × 0·25–0·68	0·16–0·63 × 0·17–0·42
Ovary (mm)	0·23–0·67 × 0·23–0·48	0·19–0·34 × 0·16–0·39
Eggs (μm)	46–53 × 25–29	44–50 × 23–32

Antero-dextrally to the testes lies a multilobate *ovary*, which may or may not be separated from the testes by coils of the uterus. Mehlis' gland is present just anterior to the ovary, and prior to reaching it the oviduct receives Laurer's canal and the common vitelline duct (Fig. 6e). Laurer's canal opens dorsally at the level of the ovary. The initial coils of the *uterus* form a large uterine seminal receptacle, which lies immediately anterior to the ovary and then passes back laterally to the testes. The remainder of the uterus, containing numerous operculate eggs with smooth shells, fills most of the post-testicular region of the hindbody. It initially passes back close to the posterior extremity and then runs forward forming transverse loops which reach close to the lateral margins of the body. At the level of the gonads the uterus becomes confined to the inter-caecal region, and, after passing dorsally to the ventral sucker, it enters the genital atrium from the left side through a muscular metraterm. The *vitellarium* consists of two lateral fields of many small follicles, which extend from about the level of the posterior margin of the posterior testis to the posterior margin of the ventral sucker. In one of the larger specimens these fields are broken up into three quite widely separated groups (Fig. 6a). The main lateral vitelline ducts unite close to Mehlis' gland, forming the common vitelline duct which is dilate proximally and acts as a vitelline reservoir.

DISCUSSION. A comparison of our material from the NE Atlantic with that of Campbell (1975) leaves no doubt that they belong to the same species. There are, however, minor differences between our material and Campbell's description; but these can be explained by differences in interpretation and fixation techniques. Campbell, for example, describes spines in the genital atrium, and has illustrated them for us (Campbell, in litt.): we believe, however, that they are not in fact spines, but hyaline filamentous structures formed initially as a lining of the pars prostatica and which act as precursors of the wall of the spermatophore. These filamentous structures, which often extend from the pars prostatica, through the ejaculatory duct and into the genital atrium, are essentially the same in all of the fellodistomines. Our material also differs in configuration of the uterus, in that the uterine coils overlie the caeca in the post-testicular region. It seems that the inter-caecal condition reported by Campbell is an artifact produced by flattening the worms during fixation, as Campbell's sectioned material shows the uterus extending ventrally to the caeca in the post-testicular region.

Steringophorus thulini sp. nov.

TYPE-HOST AND LOCALITY. *Onogadus argentatus*, N of Rona, Scotland (60°N, 06°W).

RECORDS

(i) Material studied

(a) From NE Atlantic

Onogadus argentatus [intestine] N of Rona, Scotland (60°N, 06°W; depth 1090–1110 m; April, 1973). BM(NH) (Holotype) 1977.3.16.1. (Paratypes) 1977.3.16.2–5.

Rhinonemus cimbrius [intestine] Mid-Skagerrak, between Denmark & Sweden (Dec., 1970). Material of J. Thulin.

Trachyrincus trachyrincus [rectum] St Kilda region, Scotland (58°N, 10°W; depth 1300–1330 m; Oct., 1978). BM(NH) 1979.2.14.4–6.

(b) From elsewhere

None

(ii) NE Atlantic records from the literature

None

ASPECTS OF BIOLOGY. Nothing is known about the biology of this species, except that it occurs in the intestine of gadoids. *S. furciger* is the only other species of the genus purported to occur in gadoids from the NE Atlantic, but it appears likely that these records are questionable or accidental.

PREVIOUS DESCRIPTIONS

None.

DESCRIPTION (Fig. 7). Five specimens from *O. argentatus*, three were serially sectioned after being measured, three from *T. trachyrincus*, one was sectioned, and one specimen from *R. cimbrius* were studied. The worms are fusiform when young (Fig. 7b), but the hindbody widens allometrically in older worms (Fig. 7a, c). The body-surface is smooth. Both suckers are globular, and, as can be seen from the dimensions of this species given in Table 6, the subterminal *oral sucker* is consistently slightly smaller than the *ventral sucker*, which lies at about one-third of the body-length from the anterior end. A short prepharynx (seen only in sections), a globular *pharynx* and a distinct oesophagus form the anterior part of the alimentary system. In about the middle of the forebody the intestine bifurcates and the narrow caeca extend back to about the middle of the post-testicular region.

The *excretory pore* is terminal and leads into a 'Y'-shaped vesicle, the stem of which forms a flattened sac. At the testicular level it divides, forming two wide arms which reach into the forebody approximately to the level of the pharynx.

The large *testes* lie symmetrically in the anterior half of the hindbody. They have deeply indented margins. The vasa efferentia pass separately, but close together through the wall of the cirrus-sac. The oval *cirrus-sac* is present in the posterior region of the forebody slightly overlapping the anterior margin of the ventral sucker. It normally contains a large bipartite seminal vesicle, wide pars prostatica with filamentous lining and short, wide, pocketed ejaculatory duct (Fig. 7d). In one sectioned specimen, however, the ejaculatory duct is apparently everted and the contents of the cirrus-sac are distorted. The seminal vesicle of this worm is almost empty and, although it gives the appearance of being bipartite, it is not easy to distinguish where the pars prostatica begins. It would appear, however, that the most distal part of the duct is probably the

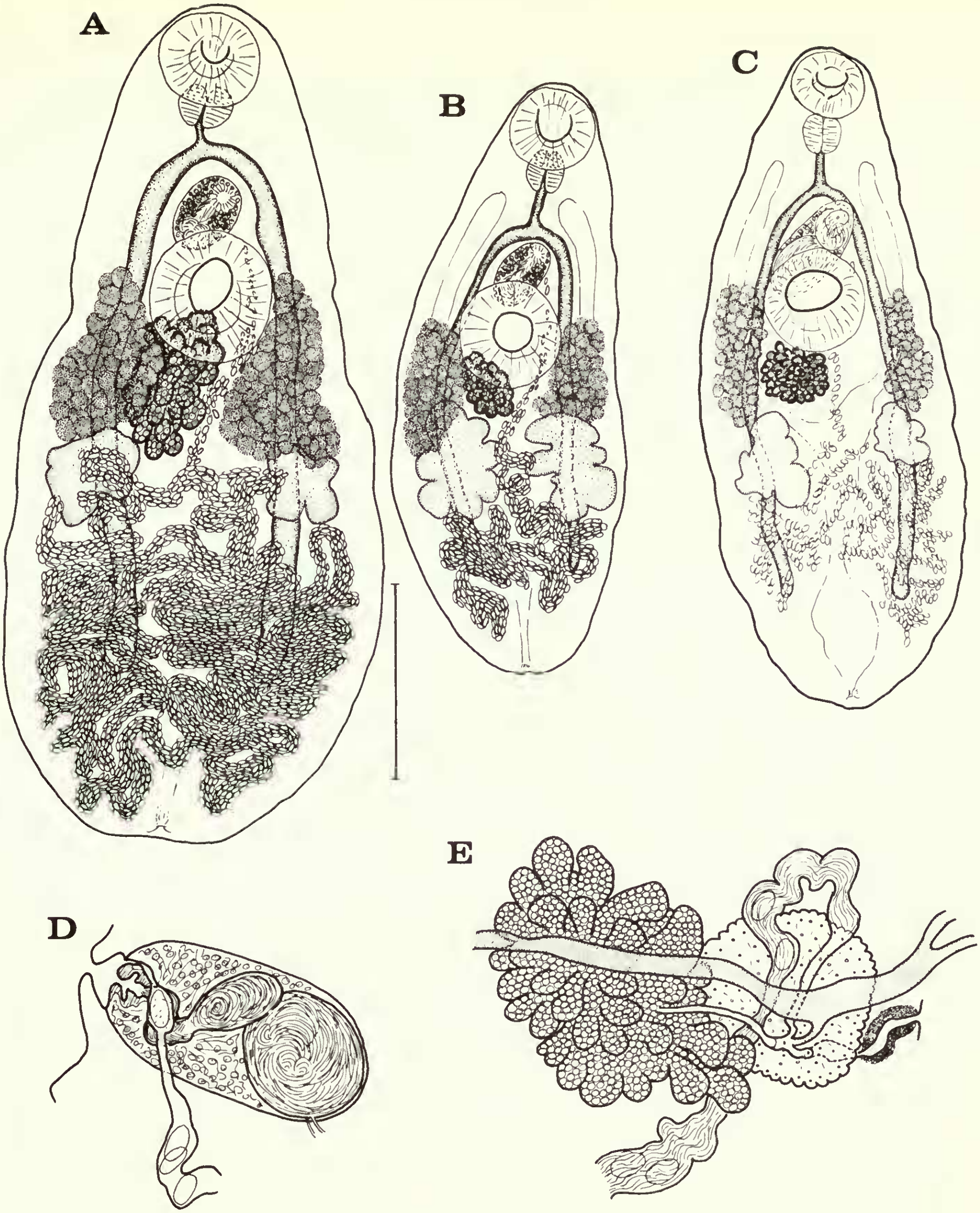

Fig. 7 *Steringophorus thulini*: (a & b) specimens from *Onogadus argentatus*; (c) specimen from *Trachyrincus trachyrincus*; (d) cirrus-sac; (e) diagram of female proximal genitalia. Bar scale: a, b, c = 0·5 mm.

pars prostatica, as the prostatic cells appear to arise from this region. There is little evidence of the ejaculatory duct, and we must assume that it has become the external wall of the genital papilla or cirrus. It seems likely that this specimen has ejaculated shortly prior to being fixed, and that the missing filamentous lining to the pars prostatica probably formed the wall of the spermatophore. The genital atrium is normally larger than is usual in this subfamily, and possesses a wide pore lying slightly sinistrally immediately posterior to the intestinal bifurcation.

Table 6 Dimensions of *Steringophorus thulini*

Host	*Onogadus argentatus*	*Rhinonemus cimbrius*	*Trachyrincus trachyrincus*
Locality	Scotland	Skagerrak	Scotland
Length (mm)	1·46–2·15	1·65	1·7–1·85
Breadth (mm)	0·60–1·00	0·90	0·74–0·86
Length : forebody ratio	1 : 0·26–0·34	1 : 0·42	1 : 0·27–0·31
Oral sucker (mm)	0·16–0·24 × 0·18–0·24	0·20 × 0·22	0·16–0·18 × 0·16–0·21
Ventral sucker (mm)	0·21–0·33 × 0·21–0·32	0·22 × 0·26	0·24–0·30 × 0·28–0·30
Sucker-ratio	1 : 1·2–1·3	1 : 1·1	1 : 1·43–1·75
Pharynx (mm)	0·099–0·124 × 0·103–0·128	0·12 × 0·09	0·07–0·11 × 0·09–0·11
Oesophagus (mm)	0·065–0·103	0·15	0·10–0·14
Cirrus-sac (mm)	0·16–0·23 × 0·14–0·15	*c.* 0·19 × 0·11	0·24–0·32 × 0·13–0·14
Testes (mm)	0·18–0·28 × 0·20–0·28	0·19–0·23 × 0·19–0·25	0·18–0·27 × 0·16–0·20
Ovary (mm)	0·17–0·27 × 0·20–0·40	*c.* 0·23 dia.	0·19–0·22 × 0·24–0·29
Eggs (μm)	36–43 × 20–23 (usually 38–42 × 20–22)	42–43 × 21–24	37–47 × 18–22 (usually 38–41 × 20–22)

The large, multilobate *ovary* lies antero-medially to the right testis, and may be overlapped anteriorly by the posterior margin of the ventral sucker. A large, prominent Mehlis' gland lies to the left of the ovary and, just prior to entering it, the oviduct receives Laurer's canal and the common vitelline duct (Fig. 7e). Laurer's canal follows a convoluted course and opens dorsally at about the level of the ovary. There is no seminal storage organ associated with Laurer's canal, but the proximal end of the *uterus* forms a uterine seminal receptacle. The bulk of the narrow, convoluted uterus, which contains numerous smooth-shelled, operculate eggs, occupies most of the post-testicular region of the hindbody in the form of a mass of convoluted tubules that extends extra-caecally. The last coils are inter-testicular, after which it passes forward directly towards the genital atrium which it enters laterally through a narrow metraterm. The *vitellarium* consists of two lateral fields of closely packed follicles lying between the middle of the ventral sucker and the anterior margin of the testes and often overlapping the caeca ventrally. The follicles feed two main lateral collecting ducts which unite to form a common duct just ventrally to Mehlis' gland.

DISCUSSION. This species is most similar to *S. foliatus* (Yamaguti, 1970) comb. nov., from the intestine of *Emmelichthyops* sp. off Hawaii, for which Yamaguti (1970) created the new genus *Callodistomoides*. It can, however, be distinguished from this species by its shorter caeca, smaller eggs and slightly larger vitelline field.

The specimens from *T. trachyrincus* show slight differences from those in the other hosts. The cirrus-sac is consistently larger and the sucker-ratio is greater. These do not appear to be features which would make it necessary to consider them as belonging to a different species. In the collections of the British Museum (Natural History) there is a similar mature worm from *Lepidion eques* in Newfoundland (BM(NH) 1967.6.19.1, collected by W. Templeman). It has a sucker-ratio of 1 : 2·1 and the only undeformed egg is 48 × 22 μm. An immature specimen has a sucker ratio of 1 : 1·7.

We have named this species in honour of Mr Jan Thulin, University of Gothenburg, Sweden, as an expression of thanks for all the help which he has given us by providing material from his collections, both of this group and others in the series.

Genus ***OLSSONIUM*** gen. nov.

DEFINITION. Body small; fusiform. Body-surface smooth. Oral sucker subterminal; globular. Ventral sucker in anterior half of body; similar in size to oral sucker. Prepharynx small but distinct. Pharynx small. Oesophagus short. Caeca narrow; reaching almost to testes. Testes oval;

more or less symmetrical; in anterior hindbody. Cirrus-sac large; containing bipartite seminal vesicle, wide pars prostatica with filamentous lining and external gland-cells, and wide, diverticulate ejaculatory duct. Genital atrium large. Genital pore ventral in posterior forebody; slightly sinistral. Ovary trilobed; anterior to right testis and postero-dextral to hind margin of ventral sucker. Laurer's canal and uterine seminal receptacle present. Uterus coils in post-testicular region, in inter-testicular region and dorsally to ventral sucker. Eggs small; operculate; with smooth shell, but may have small boss at one or both ends. Vitellarium follicular; in two lateral fields in forebody. Excretory vesicle 'Y'-shaped; with wide stem bifurcating at level of testes to give rise to two dilate arms which extend into forebody. Parasitic in intestine of marine teleosts.

TYPE-SPECIES. *Olssonium turneri* sp. nov.

COMMENT. This genus differs from *Steringophorus* notably in the distribution of the vitellarium and the shape of the ovary. Other similar fellodistomid genera which possess a 'Y'-shaped excretory vesicle are *Hypertrema* Manter, 1960, *Pseudosteringophorus* Yamaguti, 1940, and *Benthotrema* Manter, 1934. *Hypertrema* has a double egg-shell and a cirrus-sac which is often constricted in the middle, the distal part being bulbous and containing the ejaculatory duct, pars prostatica and one section of the tripartite seminal vesicle. The narrower proximal portion contains two further sections of the seminal vesicle (Overstreet & Martin, 1974). The vitelline fields unite medially in the forebody and the ovary, which consists of three rounded and distinctly separate parts ('ovaries 3' – Overstreet & Martin, 1974), lies medially to the right testis. *Hypertrema* is also said to possess a large, muscular papilla in the genital atrium, but this may be part of the ejaculatory duct, as described in other fellodistomines. Bilqees (1976) considers her new genus *Pseudohypertrema* to be similar to *Hypertrema*. Unfortunately, the shape of the excretory vesicle of *Pseudohypertrema* was not described; but it differs from *Olssonium* in a number of features, notably the double-shelled nature of the eggs, the inter-testicular and sub-globular ovary, the confluent vitelline fields, the caeca extending into the post-testicular region and the morphology of the cirrus-sac. *Pseudosteringophorus* has an oval ovary, a single vitelline field, a long oesophagus and a thin-walled cirrus-sac; but it is obviously similar to *Olssonium*. *Benthotrema* is also similar, especially when the species added to the genus by Yamaguti (1938) and Manter (1954) are considered. Manter (1934) did not describe the excretory vesicle, but the later reports indicate that it is 'Y'-shaped. It differs from *Olssonium*, however, in having an oval ovary and, usually, a coiled seminal vesicle. *Benthotrema hoplognathi* Yamaguti, 1938, which has a bipartite seminal vesicle, differs, in addition to the oval ovary, in the apparent presence of a distinct seminal receptacle, a more lateral position of the genital pore and in the apparent absence of a wide, diverticulate ejaculatory duct. As this species is superficially similar to *Olssonium* and as there are certain questionable features in Yamaguti's description, e.g. the presence of a distinct seminal receptacle, it is possible that a future study of this species might show that it belongs in *Olssonium*. *Benthotrema hilsii* Zaidi & Khan, 1977, may be a species of *Faustula* Poche, 1926, many species of which have been recorded from the same host.

This genus is named in honour of the nineteenth century Scandinavian helminthologist Dr Peter Olsson, who did much valuable work on the parasites of marine fishes.

Olssonium turneri sp. nov.

TYPE-HOST AND LOCALITY. *Alepocephalus bairdii*, W of Ireland (54°N, 14°W).

RECORDS

(i) Material studied

(a) From the NE Atlantic

Alepocephalus bairdii [Upper intestine] Porcupine Bank, off western coast of Ireland (54°N, 14°W; depth 1000 m; June, 1974). BM(NH) (holotype) 1977.3.17.1 (paratype) 1977.3.17.2.

(b) From elsewhere

None

(ii) NE Atlantic records from the literature
None

Aspect of biology: This species was found sympatrically with *Steringophorus pritchardae*.

Previous descriptions. None.

Description (Fig. 8). Only two specimens were found, one of which (the paratype) was studied in serial section. Most of the measurements were taken from the single wholemount, which is

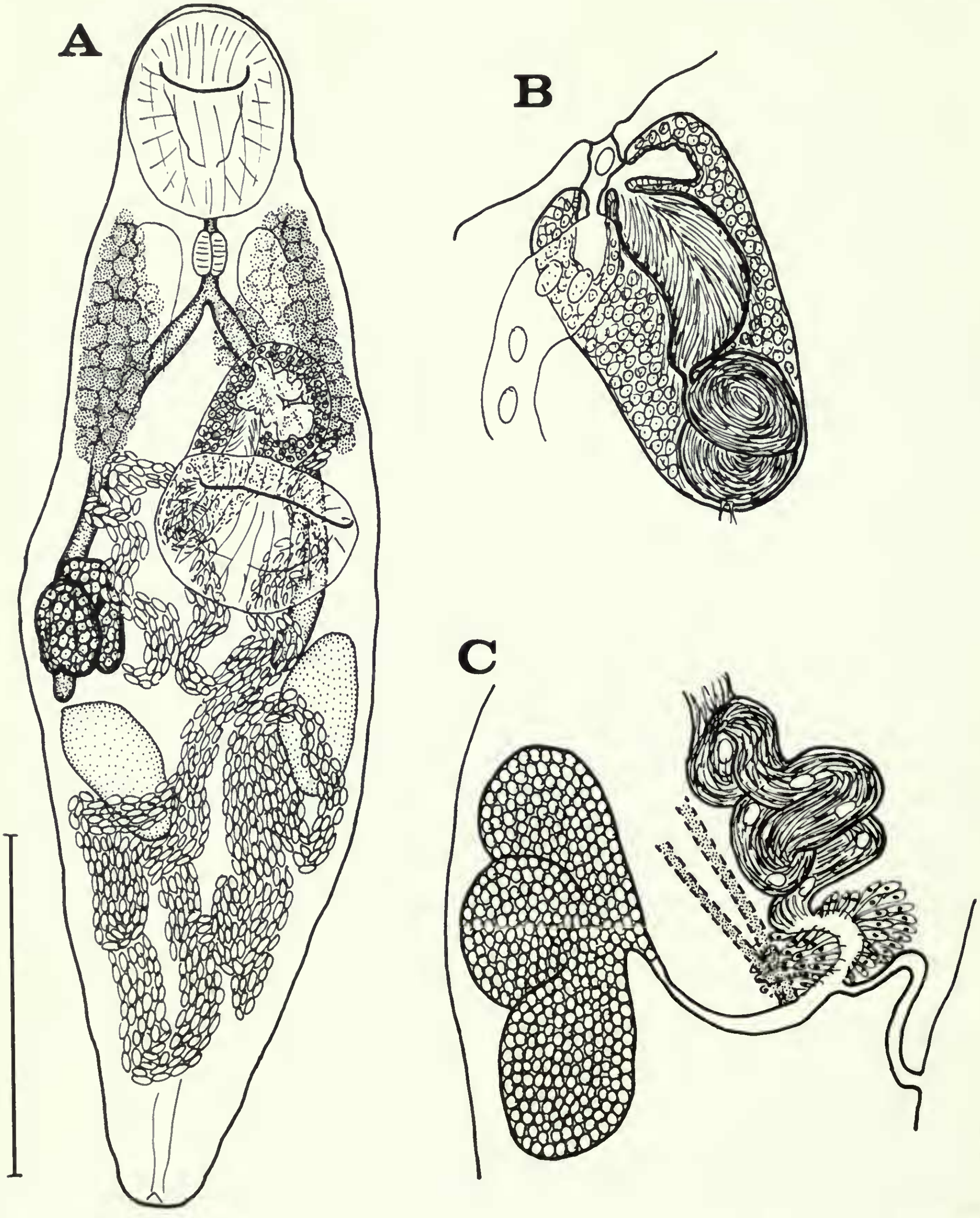

Fig. 8 *Olssonium turneri*: (a) whole-mount specimen; (b) cirrus-sac; (c) diagram of female proximal genitalia. Bar scale: a = 0.5 mm.

2·02 mm long and 0·53 mm wide at its widest point just posterior to the ventral sucker. The worm is fusiform with bluntly rounded extremities (Fig. 8a), and the body-surface is smooth. The *oral sucker* (0·29 × 0·23 mm) opens just subterminally, and is similar in size to the *ventral sucker* (0·22 × 0·29 mm), which lies just inside the anterior half of the body. The length/forebody ratio is 1 : 0·37. There is a short (0·01 mm) but distinct prepharynx which opens into a small *pharynx* (0·07 × 0·057 mm). The oesophagus is short (0·04 mm) and gives rise, in about the middle of the forebody, to two narrow caeca. These reach back approximately to the level of the anterior margin of the testes.

The *excretory pore* is terminal and leads into the wide stem of a 'Y'-shaped excretory vesicle. The stem divides at about the level of the testes, and the arms reach to the level of the pharynx, being dilate in the forebody.

The oval *testes* (0·23–0·24 × 0·11–0·13 mm) are almost symmetrically arranged, but the right testis is slightly more posterior, and the longest axis is oriented longitudinally. The vasa efferentia pass separately, but close together through the wall of the cirrus-sac. The *cirrus-sac* (0·32 × 0·18 mm) is of the typical fellodistomine type and overlaps the anterior margin of the ventral sucker. It contains a bipartite seminal vesicle, a wide pars prostatica with a filamentous liningand a wide, diverticulate ejaculatory duct, all of which are surrounded by the external gland-cells of the pars prostatica (Fig. 8b). The genital atrium is small and opens ventrally, through the genital pore, just to the left of the median line in the posterior half of the forebody.

The distinctly tri-lobed *ovary* (0·20 × 0·13 mm) is situated just anteriorly to the right testis, postero-laterally to the ventral sucker, and ventral to the right caecum. The oviduct leaves the ovary dorsally and passes towards the dorsal surface where it enters a rather amorphous Mehlis' gland. The sectioned specimen is distorted by a dorsal invagination, but it appears that prior to reaching Mehlis' gland the oviduct receives Laurer's canal and probably the common vitelline duct, although this was not seen. Laurer's canal is short and curves between its union with the oviduct and its pore which opens dorsally just posterior to Mehlis' gland (Fig. 8c). The proximal *uterus* forms a large, tightly coiled uterine seminal receptacle. The remainder of the uterus extends well into the post-testicular region, and also lies between the testes, in the pre-testicular region of the hindbody and dorsally to the ventral sucker. It joins the genital atrium from the left side via a short, narrow duct which forms the end of the wide, thin-walled metraterm. The numerous, operculate eggs (38–42 × 24–25 µm), which sometimes bear small bosses at one or both poles, have otherwise smooth shells. There are two lateral fields of tightly packed *vitelline follicles* which occur in the forebody between the anterior margin of the ventral sucker and the posterior margin of the oral sucker. They surround the arms of the excretory vesicle ventrally, laterally and dorsally. Although the left field may lie dorsally to part of the cirrus-sac the two fields do not unite medially.

DISCUSSION. It is unfortunate that the specimen chosen for sectioning was distorted in the region of the female proximal system. Much of the system could be made out, but the exact nature of the junction of the vitelline system with the oviduct was not seen.

This species is named in honour of Mr Robert J. 'Bob' Turner, of the MAFF Laboratory at Lowestoft in gratitude for his help to one of us (R. A. B.) on numerous occasions.

Genus *STERINGOTREMA* Odhner, 1911

Rhodotrema Odhner, 1911.

Yamaguti (1953*a*) points out that *Rhodotrema* has page-priority over *Steringotrema*, but suggests that as the type-species of *Rhodotrema* [*R. ovacutum* (Lebour, 1908)] is based on an immature worm, *Steringotrema* should be given preference. *R. ovacutum*, however, is not in fact based on an immature worm (see Lebour, 1908*b*); but for the sake of stability we are invoking Article 24(a) of the International Code of Zoological Nomenclature, crediting Yamaguti (1953*a*) as being the 'first reviser', and, therefore, retaining the name *Steringotrema* for this genus.

DIAGNOSTIC FEATURES. Body small to large; globular to oval. Body-surface smooth. Oral sucker globular to oval. Ventral sucker large; significantly larger than oral sucker; globular; in middle of worm. Prepharynx short. Pharynx well developed. Oesophagus short. Caeca extend back to level of testes or just beyond. Testes two; symmetrical; post-ovarian; in anterior hindbody. Cirrus-sac oval. Seminal vesicle bipartite. Pars prostatica wide; with filamentous lining. Ejaculatory duct wide; diverticulate. Genital atrium small. Genital pore median to sinistrally submedian; at about level of caecal bifurcation. Spermatophores may be present. Ovary entire to trilobate; just anterior or antero-median to right testis. Uterus mainly post-testicular; fills most of hindbody in older specimens. Eggs numerous; operculate; often with considerable variation in size; occasionally with ornamented shells. Vitellarium follicular; in two or four lateral fields between mid-forebody and level of testes; occasionally confluent dorsally. Excretory vesicle 'V'-shaped; arms reaching to pharynx. Parasitic in intestine (occasionally gall-bladder and stomach) of marine teleosts.

TYPE-SPECIES. *Steringotrema pagelli* (van Beneden, 1871) (syn. *S. cluthense* (Nicoll, 1909) – type by original designation).

COMMENT. We have not been able to find any good reason to accept *Rhodotrema* Odhner, 1911, as a valid genus distinct from *Steringotrema*. The characters which differentiate the type-species, *R. ovacutum* (Lebour, 1908), from other species of *Steringotrema* are given in the key presented below; these differences, in our opinion, do not warrant a generic distinction. The genus *Rhodotrema* has, however, been credited with a number of species in the past; but it is apparent that the following species should be considered species, or synonyms of species, of the opecoelid genus *Stenakron* Stafford, 1904, and related genera (see p. 201 and Bray, 1979):

1. *Rhodotrema problematicum* Issaitschikov, 1928
2. *Rhodotrema skrjabini* Issaitschikov, 1928
3. *Rhodotrema quinquelobatum* Layman, 1930
4. *Rhodotrema quadrilobatum* Bazikalova, 1932
5. *Rhodotrema lethrini* Yamaguti, 1938.

Of the 15 species which have been included in *Steringotrema*, we herein consider that only six are valid. They are:

(1) *Steringotrema corpulentum* (Linton, 1905) Manter, 1931; this species occurs off the south-eastern coast of the USA and in the Gulf of Mexico. It has been described by Linton (1905) and figured and commented upon by both Manter (1931) and Sogandares-Bernal & Hutton (1959). It is atypical of the genus in that it possesses a median genital pore and vitelline fields which are confluent dorsally.

(2) *Steringotrema divergens* (Rudolphi, 1809) Odhner, 1911; see p. 239.

(3) *Steringotrema ovacutum* (Lebour, 1908) Yamaguti, 1953; see p. 242.

(4) *Steringotrema pagelli* (van Beneden, 1871) Odhner, 1911; see p. 234.

(5) *Steringotrema phrissovum* (Aldrich, 1961) n. comb.; from the intestine of *Parophrys vetulus* off Washington State, USA. It was originally placed in *Fellodistomum;* but the uterus has several loops in the post-testicular region, the excretory vesicle is 'V'-shaped and the eggs are 'spiny', i.e. ornamented. In addition, the ovary is lobate (the figure suggests that it might be trilobed) and the worm bears a considerable resemblance to *S. ovacutum* from which it differs in egg-size.

(6) *Steringotrema rotundum* Manter, 1954; from the gall-bladder and stomach of *Parapercis colias* off New Zealand. It differs from the other species of the genus in having the vitellarium confined to the region posterior to the middle of the ventral sucker. Yamaguti (1971) considered it to be a *Fellodistomum*; but Armstrong (1974) reinstated it in *Steringotrema* and, with post-testicular uterine coils and a 'V'-shaped excretory vesicle, it would appear to fit comfortably into the latter genus.

The other species which have been included in *Steringotrema* are:

(1) *Steringotrema blennii* (Müller, 1776) Dollfus, 1968; Dollfus (1968) considered this to be the oldest available name for *S. divergens*. Müller's description and figures (Müller, 1776 : 224; 1777 : pl. 30, fig. 5; 1780 : pl. 78, figs 9–12; and 1784 : 116 – see Anker, 1950) show clearly that it is not the same species as *S. divergens* of Rudolphi (1809) as seen and redescribed by Odhner (1911*a*) . In our opinion *Fasciola blennii* of Müller is unrecognizable.

(2) *Steringotrema cluthense* (Nicoll, 1909) Odhner, 1911; original type-species of the genus, herein considered to be a synonym of *S pagelli* (see p. 238).

(3) *Steringotrema crassum* (Manter, 1934) Yamaguti, 1953; this species, originally considered as the type-species of the genus *Megenteron* Manter, 1934, differs from *Steringotrema* in possessing long, wide caeca reaching to the posterior extremity of the long hindbody, a small ventral sucker and a multilobate ovary.

(4) *Steringotrema nakazawai* Kobayashi, 1920; this species occurs in sparid fishes in Japanese waters and has been described by Kobayashi (1920) and Yamaguti (1934: 1938). It is superficially similar to *S. pagelli* (particularly the 'small egg' form), although its sucker-ratio is at the extreme end of the range of this species (Kobayashi's measurements suggests an oral to ventral sucker-ratio of 1 : 5–10, but his figure indicates a ratio of 1 : 3·5. Yamaguti's measurements give ratios of 1 : 4 in 1934 and 1 : 5·2 in 1938). The lobed ovary is said to lie posteromedially to the right testis, an unusual position in this subfamily, and the vitellarium is broken up into 5 or 6 bunches of follicles on each side of the body (Kobayashi, 1920; Yamaguti, 1938). Skrjabin & Koval (1957) use this species as the type of a new genus *Markevitschiella*, and created a new subfamily, the Markevitschiellinae, which differs from the Fellodistominae in the following: 'ventral sucker four to five times larger than oral sucker; loops of uterus in one side of body' (Skrjabin *et al.*, 1964). Although Kobayashi's figure does suggest that the uterus is confined to the left side of the body, his description indicates that this feature may not be significantly different from that of species of *Steringotrema* where the uterus fills most of the hindbody and passes anteriorly on the left side of the body toward the genital atrium. Furthermore, Yamaguti (1938) states 'uterus coiled at posterior end of body and on left of the acetabulum'. With regard to the sucker-ratio, we do not consider it alone to be a feature of generic importance. We are, however, reluctant either to accept or to reject *Markevitschiella* on the evidence in the literature. If the position of the ovary and the divided nature of the vitellarium are constant features, then the genus may be valid.

(5) *Steringotrema ovata* Price, 1934; possibly a species of *Bacciger* (see p. 249).

(6) *Steringotrema ponticum* (Pigulewsky, 1938) Yamaguti, 1953; this species was described briefly by Pigulewsky (1938) from *Engraulis encrasicolus* in the Black Sea as the type-species of the new genus *Ovotrema*. It is possible that this species may be a *Steringotrema*, but the ovary is described as medial and slightly post-testicular. Skrjabin & Koval (1957) and other Soviet workers have considered it a synonym of *Bacciger bacciger* (Rudolphi, 1819) and Yamaguti in a recent work (1971) has followed this; but Margolis & Ching (1965) have argued against this synonymy. It is clear that due to an initial inadequate description the status of this species must remain unresolved; but, at least for the present, we prefer to accept it as a questionable synonym of *B. bacciger* (see p. 254 and p. 259).

(7) *Steringotrema pulchrum* Johnston, 1913; this species was considered to belong to the genus *Lintonium* Stunkard & Nigrelli, 1930, by Skrjabin & Koval (1957), as a synonym of what is now *L. consors* (Lühe, 1906) by Odhner (1928) and as a distinct species of the latter genus by Manter & Pritchard (1962).

(8) *Steringotrema quadrilobatum* (Bazikalova, 1932) Yamaguti, 1958; see above under *Rhodotrema* (p. 232).

(9) *Steringotrema quinquelobatum* (Layman, 1930) Yamaguti, 1953; see above under *Rhodotrema* (p. 232).

Key to the species of *Steringotrema* recorded from the northeast Atlantic

1 Vitellarium divided into 4 zones; ovary globular . . ***S. divergens*** (Rudolphi, 1809) (p. 239)
– Vitellarium divided into 2 lateral zones; ovary trilobed 2
2 Vitellarium reaching back to middle of ventral sucker; egg-shell prominently ornamented . . . . ***S. ovacutum*** (Lebour, 1908) (p. 242)
– Vitellarium reaching back to level of testes; egg-shell smooth or *very* weakly ornamented . . . . ***S. pagelli*** (van Beneden, 1871) (p. 234)

Steringotrema pagelli (van Beneden, 1871) Odhner, 1911

Distoma pagelli van Beneden, 1871.
Steringotrema (*Ovotrema*) *pagelli* (van Beneden) Yamaguti, 1953.
Distomum tergestinum Stossich, 1888.
Steringophorus cluthensis Nicholl, 1909.
Leioderma cluthense (Nicoll) Nicoll, 1910.
Steringotrema cluthense (Nicoll) Odhner, 1911.

TYPE-HOST AND LOCALITY. *Pagellus bogaraveo*, Louvain, Belgium.

RECORDS
(i) Material studied
(a) From the NE Atlantic

Mature worms

Limanda limanda [?] Carmarthen Bay, Dyfed, Wales (Sept.–Nov., 1976). Collected H. Al-Abdul-Jabbar. BM(NH) 1977.5.9.1–3.

Microstomus kitt [intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1977.5.10.1.

—— [intestine] Lossiemouth, Grampian Region, Scotland (Oct., 1973). BM(NH) 1977.5.10.2–11.

Spondyliosoma cantharus [intestine] Whitby, North Yorkshire, England. Collected by G. A. Boxshall. BM(NH) 1976.1.7.10.

—— [intestine, pyloric caeca] Southern North Sea (Nov., 1960). BM(NH) 1978.1.18.1–15.

—— ['gut'] Scarborough, North Yorkshire, England (Oct., 1976; Nov., 1977; Nov., 1978). Collected by D. Whittaker. BM(NH) 1979.2.14.12–19.

Immature worms

Limanda limanda [stomach & intestine] Plymouth, Devon, England (May, 1932), (see Baylis & Jones, 1933; Baylis, 1939; as *S. cluthense*), BM(NH) 1932.11.25.9 (see Baylis & Jones, 1933; Baylis, 1939, as *Steringophorus furciger*), BM(NH) 1932.11.25.1–8 [intestine] (March, 1969), BM(NH) 1972.3.27.18; (May, 1972), BM(NH) 1977.5.10.2–14.

Microstomus kitt [stomach & intestine] Plymouth, Devon, England (May, 1932) (see Baylis & Jones, 1933; Baylis, 1939; as *S. cluthense*), BM(NH) 1932.11.25.10–11; [intestine] (May, 1972), BM(NH) 1977.5.10.15–19.

—— [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

—— [pyloric caeca] Moray Firth, Scotland (58°N, 02°W; depth 90–102 m; July, 1976). BM(NH) 1977.5.10.20.

Pleuronectes platessa [intestine] Tjärnö, Sweden (June, 1971). Material of J. Thulin.

—— [intestine] Kristineberg, Sweden (Dec., 1971). Material of J. Thulin.

—— [intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1977.5.10.21.

(b) From elsewhere
None

(ii) NE Atlantic records from the literature

Limanda limanda [stomach & intestine] Plymouth, Devon, England (May, 1932). Baylis & Jones (1933 : 630; as *S. cluthense* and *Steringophorus furciger*); Baylis (1939 : 482; as *S. cluthense* and *Steringophorus furciger*).

Microstomus kitt [duodenum & pyloric caeca] Firth of Clyde, Scotland, Nicoll (1909*a* : 472; as *Steringophorus cluthense*; 1910 : 347; as *Leioderma cluthense*).

—— [intestine] Plymouth, Devon, England. Nicoll (1914 : 478, 502; as *S. cluthense*); [stomach & intestine] (May, 1932) Baylis & Jones (1933 : 630; as *S. cluthense*); Baylis (1939 : 482; as *S. cluthense*).

—— [intestine] Galway, Ireland. Little (1929 : 26, 27; as *S. cluthense*).

Pagellus bogaraveo [stomach] Louvain, Belgium. van Beneden (1871 : 43; as *Distoma pagelli*).

—— [intestine] Billingsgate Fish Market, London (material either from North Sea or from English Channel). Nicoll (1914 : 480).

—— [intestine] Plymouth, Devon, England. Nicoll (1914 : 497).
—— [intestine] Galway, Ireland. Little (1929 : 26, 27).
Spondyliosoma cantharus [pyloric caeca & intestine] Ostende, Belgium. van Beneden (1871 : 43; as *Distoma pagelli*).

Aspects of biology. This species infests, in its adult form, two or three species of flatfish and members of the family Sparidae. It is not known what causes this unusual spread of hosts. All the adult worms we have examined have been found late in the year (September–November), with the exception of one early mature specimen collected at Plymouth in May. In addition to its being found in the northeastern Atlantic as far north as Sweden, this species has also been recorded in the Mediterranean and once (Ronald, 1960) from the Gulf of St Lawrence.

It is apparent that sperm-transfer involves the use of spermatophores (Fig. 9c).

Previous descriptions. van Beneden (1871 : figure only; as *Distoma pagelli*); Stossich (1888 : 102; 1889 : 28; as *Distoma tergestinum*); Nicoll (1909*a* : 472; as *Steringophorus cluthense*); Odhner (1911*a* : 102); Nicoll (1914 : 480); Lopez-Roman & Guevara-Pozo (1974 : 1).

Description. (Figs 9 & 10). Forty-seven whole-mounted mature worms (seven of which were flattened) and 52 whole-mounted immature worms were studied along with six sets of serial sections. These worms are small with a broad pyriform body, the anterior region of which tapers towards a pointed pre-oral lobe under certain fixation conditions (Fig. 9b). The posterior end is rounded, although occasionally bearing a small terminal boss (Figs 9a, b & 10a, b). The dimensions of the worms are given in Table 7. The body surface is smooth. The subglobular *oral sucker* opens subterminally and is much smaller than the large, muscular *ventral sucker*, which is slightly wider than long and lies, deeply embedded, more or less in the middle of the body. In immature worms the sucker-ratio shows a continuous gradation down to a minimum of 1 : 1·3, but in adult worms the sucker-ratio is usually greater than 1 : 2. There is a short prepharynx leading to a subglobular *pharynx*. The oesophagus is distinct and its length is quite variable. It divides at about the middle of the forebody. The caeca reach into the hindbody, passing dorso-laterally

Table 7 Dimensions of *Steringotrema pagelli* from the present material

Hosts	*Limanda limanda*	*Microstomus kitt**	*Microstomus kitt*	*Spondyliosoma cantharus*	*Spondyliosoma cantharus*
Locality	Wales	Plymouth	Lossiemouth	Whitby	North Sea
Length (mm)	1·20–1·85	1·16	1·00–1·15	0·85–1·3	1·08–2·3
Breadth (mm)	0·8–1·0	0·62	0·53–0·62	0·76–1·16	0·64–1·42
Length : forebody ratio	1 : 0·20–0·42	1 : 0·25	1 : 0·31–0·36	1 : 0·20–0·27	1 : 0·25–0·42
Oral sucker (mm)	0·19–0·24 × 0·19–0·21	0·16 × 0·10	0·14–0·10 × 0·13	0·14–0·16 × 0·16–0·23	0·17–0·30 × 0·19–0·33
Ventral sucker (mm)	0·49–0·60 × 0·56–0·66	0·38 × 0·46	0·33–0·36 × 0·36–0·40	0·39–0·64 × 0·52–0·87	0·43–0·80 × 0·46–1·34
Sucker-ratio	1 : 2·9–3·1	1 : 4·6	1 : 3·1–4·5	1 : 3·2–3·8	1 : 2·4–4·2
Pharynx (mm)	0·14 × 0·11–0·12	0·10 × 0·08	0·10 × 0·10	0·07 × 0·10	0·12–0·16 × 0·11–0·16
Oesophagus (mm)	up to 0·145	0·045	0·042	–	0·05–0·16
Cirrus-sac (mm)	0·25–0·29 × 0·15–0·19	0·22 × 0·11	0·18 × 0·12–0·14	0·28–0·35 × 0·12–0·18	0·28–0·44 × 0·15–0·22
Testes (mm)	about 0·20–0·21 dia.	0·17–0·22 × 0·16	–	–	0·17–0·19 × 0·14–0·19†
Ovary (mm)	about 0·12–0·13 across	0·15 × 0·08	–	–	0·18 × 0·11†
Eggs (µm)	43–49 × 31–32	61 × 36	46–66 × 32–46	44–53 × 30–34	48–59 × 31–39

* Mature specimen only.
† Only visible in small specimens.

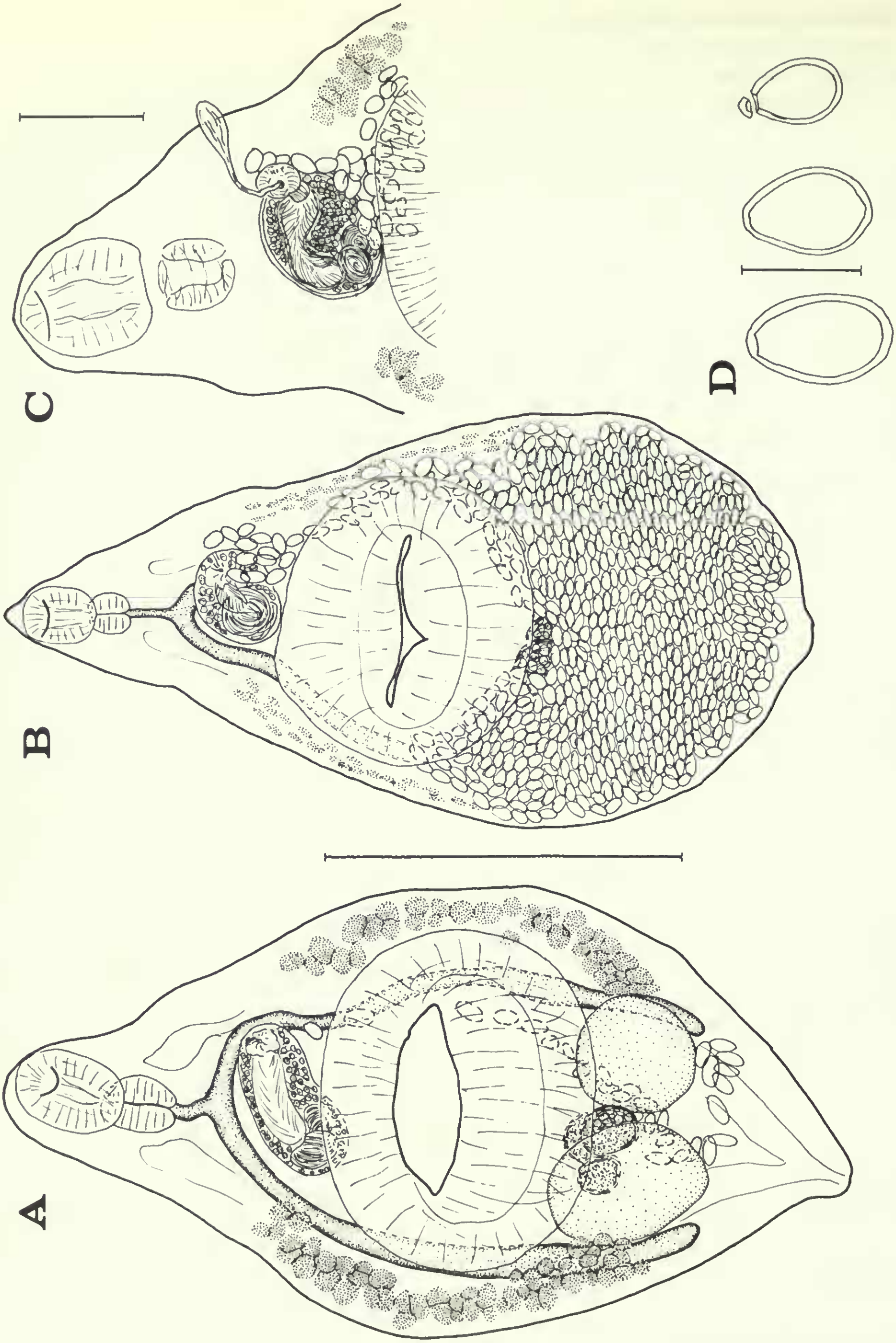

Fig. 9 *Steringotrema pagelli:* (a) young mature specimen from *Microstomus kitt*, Plymouth, May; (b) fully mature specimen from *M. kitt*, Lossiemouth, October; (c) Forebody showing cirrus-sac expelling spermatophore, from *Limanda limanda*, Carmarthen Bay; (d) eggs – left, weakly tanned from *M. kitt*, Plymouth, May; centre, strongly tanned from *M. kitt*, Lossiemouth, October; right, strongly tanned, operculum detached, from *Limanda limanda*. Bar scales: a, b = 0·5 mm; c = 0·2 mm; d = 50 µm.

to the testes, and terminate just at or beyond the posterior margin of the testes, often after having curved ventrally to a position close to the ventral surface of the hindbody.

The *excretory pore* leads into a small spherical chamber from which arise the wide arms of the excretory vesicle. These pass into the forebody, dorsally to the caeca and terminate at the level of the pharynx. Thus the overall pattern is more or less 'V'-shaped.

The *testes* are globular to oval and lie almost symmetrically close to or overlapping the posterior margin of the ventral sucker in the ventral plane. The vasa efferentia pass through the wall of the cirrus sac separately but close together. The *cirrus-sac* is oval and lies close to the anterior margin of the sucker. It contains a bipartite seminal vesicle, a wide, curved pars prostatica and a wide, diverticulate ejaculatory duct (Fig. 10c). The ejaculatory duct may form a cirrus which protrudes through the genital atrium and apparently ejects spermatophores (Fig. 9c). The genital atrium is large, and diverticulate like the ejaculatory duct. Just within the posterior half of the forebody the genital pore opens about midway between the media line and the left margin of the body.

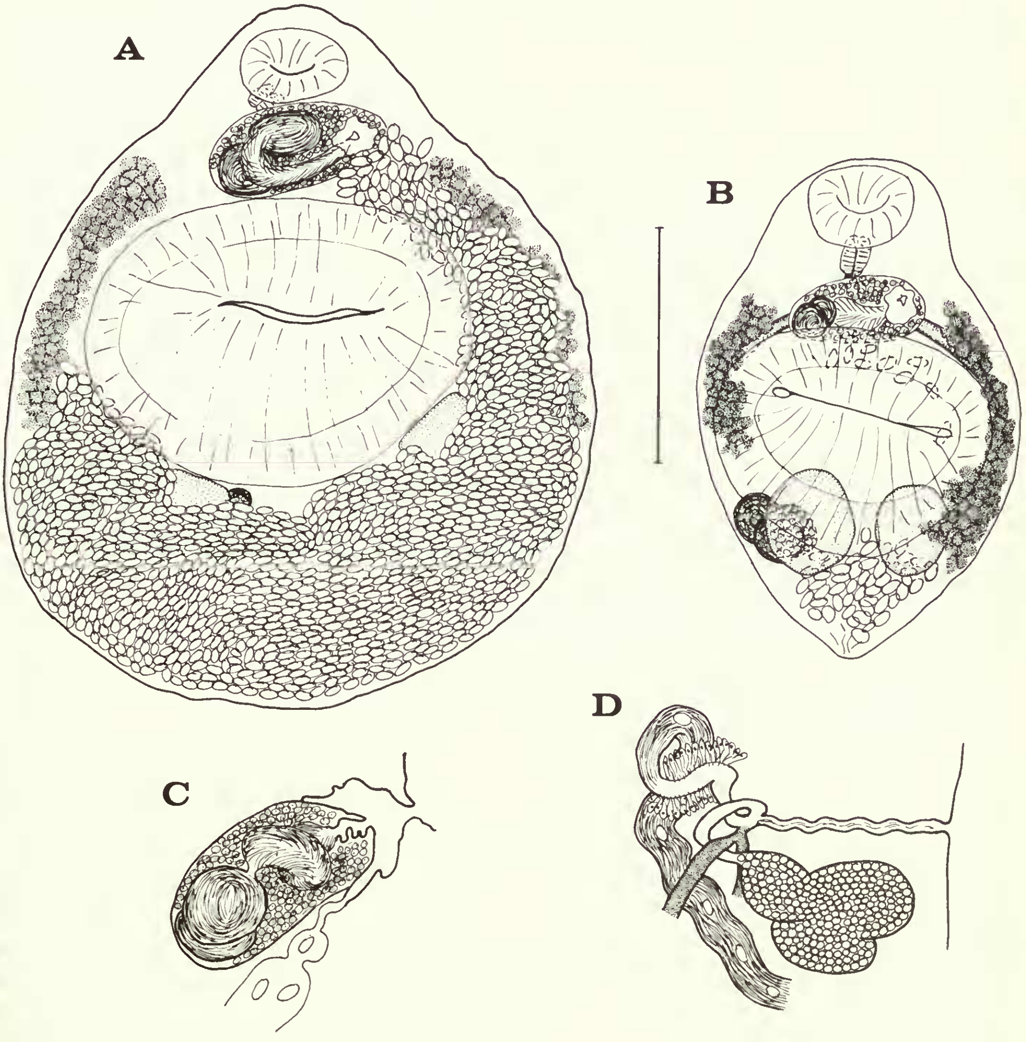

Fig. 10 *Steringotrema pagelli:* (a) flattened specimen from *Spondyliosoma cantharus*, Whitby; (b) young mature specimen, fixed *in situ*, from *S. cantharus*, southern North Sea; (c) cirrus-sac; (d) diagram of female proximal genitalia. Bar scale: a, b = 0·5 mm.

The *ovary* is divided into three irregular lobes and lies dorso-medially or dorso-laterally to the right testis. The oviduct passes ventrally and loops dorsally to a point where it receives Laurer's canal and, apparently, a short common vitelline duct. Laurer's canal is long and wide, containing evidence of spent spermatozoa and ova, and opens dorsally at the level of the ovary (Fig. 10d). Mehlis' gland lies ventrally to the ovary and from it the initial coil of the uterus passes anteriorly and then dorsally and posteriorly to almost envelope the ovarian complex in wide coils packed with spermatozoa. The *uterus* almost completely fills the hindbody in mature specimens, usually obscuring the gonads, and reaching to the posterior extremity. At the level of the ventral sucker it runs forward on the left side of the body and opens into the left side of the genital atrium through a weakly muscular metraterm. In newly mature worms the uterus is initially a single loop which extends into the post-testicular region (Fig. 9a), but in later maturity the uterus occupies much of the hindbody. The numerous eggs are variable in size, being weakly tanned and large in the single mature specimen collected early in the year at Plymouth; but in older worms eggs from the distal region of the uterus are deeply tanned and small, although those in the proximal uterus are weakly tanned and larger. Allowance must be made, therefore, when considering egg measurements, for the state of maturity and the region of the uterus from which the eggs are taken. The eggs, which tend to taper towards the opercular pole (Fig. 9d), have shells which are thick and usually appear smooth, but under very high power optical microscopy some may be seen to be very weakly ornamented. The *vitellarium* consists of two narrow lateral bands of numerous, tightly-packed follicles extending into the forebody to about the level of the genital pore. The posterior limit is often obscured by eggs, but where it can be seen it normally reaches a level between the posterior margin of the ventral sucker and the posterior margin of the testes. Sometimes the posterior termination of the vitellarium is asymmetrical, with one side terminating much further forward than the other (Fig. 10b).

DISCUSSION. The information currently available concerning this species suggests that there are two forms with distinctly different egg-sizes. van Beneden (1871) figured, but did not describe, his material, so the only useful quantitative information which his work provides are the ratios. The egg-measurements were first given by Nicoll (1909*a*) as 44–56 × 28–32 μm from *Microstomus kitt* in the Firth of Clyde, and Odhner (1911*a*) as 48–51 × 28 μm, the hosts being *Cantharus lineatus* and *C. orbicularis* (both now considered synonyms of *Spondyliosoma cantharus*) from Trieste. Shortly afterwards Nicoll (1914) redescribed the species from *Sparus centrodontus* (now *Pagellus bogaraveo*) with eggs of 57–63 × 33–37 μm. His material was collected from Billingsgate Fish Market in London and he was unable to ascertain whether the fish were caught in the North Sea or the English Channel. On page 497 of his paper, however, he lists this host and parasite as having been collected by him at Plymouth. The most recent description of this species is by Lopez-Roman & Guevara-Pozo (1974) from *Spondyliosoma cantharus* in the Mediterranean Sea off Granada, Spain. They quote the egg-size as being 58–60 × 34–36 μm. Our own specimens have eggs ranging from 43–66 × 30–49 μm. A similar variation in egg-size is found in a number of fellodistomines, such as *Steringophorus furciger*, so it would appear that this feature must be treated with a certain amount of caution. As the organs in the hindbody are obscured in fully developed specimens, there must be an inclination towards describing, and thus measuring, the eggs of younger specimens with few eggs in the uterus (see fig. 1 of Lopez-Roman & Guevara Pozo, 1974). In our material the eggs in young worms are larger and less well tanned than those from the distal region of the uterus in fully developed specimens.

Nicoll's (1909*a*) description of *S. cluthense* is the sole source of information on the morphology of that species, and our observations differ from his to some extent. He considered, however, that none of his material was fully mature, and this may account for some of the discrepancies. The sucker-ratio, which he quotes as 1 : 2, varies in our material from the same host between 1 : 1·3 and 1 : 4·6 with the mature specimens having a ratio of 1 : > 2·9. There is, therefore, obviously an allometric relationship, with the ventral sucker growing at a much faster rate than the oral sucker. The ovary was described by Nicoll as being small and multilobate; but in our material the immature specimens possess a small ovary with an indistinct irregular outline and in mature specimens this develops into a distinctly trilobed structure.

Nicoll (1909*a*) distinguished *S. cluthense* from *S. pagelli* on the sucker-ratio, the shape of the ovary, the vitelline distribution and the position of the genital atrium. Having studied specimens from both *Microstomus kitt*, the type-host of *S. cluthense*, and *Spondyliosoma cantharus*, one of the original hosts of *S. pagelli*, we have not found that any of these distinctions stand up to critical examination, as can be seen from the above description, Table 7 and Figures 9 and 10. We, therefore, consider *S. cluthense* a synonym of *S. pagelli* despite the rather different hosts usually recorded for these species.

Distoma tergestinum Stossich, 1888, from the sparid *Oblada melanura* in the Adriatic Sea off Trieste was considered a synonym of *S. pagelli* by Odhner (1911*a*), and this is accepted here. Odhner, tentatively, and Dawes (1947) also considered *Distoma actaeonis* Pagenstecher, 1862, from the sea-slug *Elysia viridis* a synonym of *S. pagelli*; but, as the description is meagre and the observation has not been repeated, we have not included it in our list of synonyms.

Steringotrema divergens (Rudolphi, 1809) Odhner, 1911

Distoma divergens Rudolphi, 1809.
Fasciola divergens (Rudolphi) de Blainville, 1820.

TYPE-HOST AND LOCALITY. *Zoarces viviparus*, Rimini, Italy.

RECORDS
(i) Material studied
(a) From the NE Atlantic
Blennius ocellaris [stomach & intestine] Plymouth, Devon, England (May, 1932) (see Baylis & Jones, 1933; Baylis, 1939), BM(NH) 1932.11.25.13–52; material collected in 1932 by J. S. Stewart, BM(NH) 1938.11.4.216–225.
Capros aper [intestine] Bay of Biscay (Jan. 1971) (see Bray, 1973). BM(NH) 1973.5.17.57–59.

(b) From elsewhere
Capros aper [intestine] Atlantic coast of Morocco (see Bray, 1973). BM(NH) 1973.5.17.57–59.

(ii) NE Atlantic records from the literature
Blennius ocellaris [stomach & intestine] Plymouth, Devon, England (June, 1910), Nicoll (1914 : 480, 499); (May, 1932) Baylis & Jones (1933 : 630), Baylis (1939 : 482).
Capros aper [intestine] Bay of Biscay (44°N, 07°W; depth 272–280 m; Jan., 1971). Bray (1973 : 173).
Ciliata mustela [intestine] Lawrenny, Dyfed, Wales (Sept., 1964). Crothers (1966 : 23).

ASPECTS OF BIOLOGY. Palombi (1931*b*) described and figured a pair of *S. divergens* in a 'pre-copulazione' condition. He also showed a 'cordono fibroso' reaching between the lumina of the ventral suckers. This may be a spermatophore, but the description is not detailed enough for us to be certain. Palombi apparently believed that copulation occurred in this species with Laurer's canal functioning as a vagina; but evidence from other fellodistomines, e.g. *Fellodistomum fellis* (see p. 206), and the presence of a uterine seminal receptacle suggests that this is extremely unlikely.

The southern region of the British Isles appears to be the northern limit of the distribution of this species, which also occurs in the Bay of Biscay, the Mediterranean Sea and the western coast of Africa as far south as Morocco and possibly Senegal. Its usual hosts are blennies and eelpouts, but recently it has been found in fishes from deeper waters, such as *Capros aper* (Bray, 1973) and a questionable record in *Pagellus bogaraveo* [the type-host of *S. pagelli*] (Fischthal & Thomas, 1972*b*).

PREVIOUS DESCRIPTIONS. Odhner (1911*a* : 103); Nicoll (1914 : 480; brief comments); Palombi (1931*a* : 1); Mathias (1934 : 567); Bray (1973 : 173); Lopez-Roman & Guevara-Pozo (1974 : 4).

DESCRIPTION (Fig. 11). This description is based upon 44 whole-mounted and three sectioned

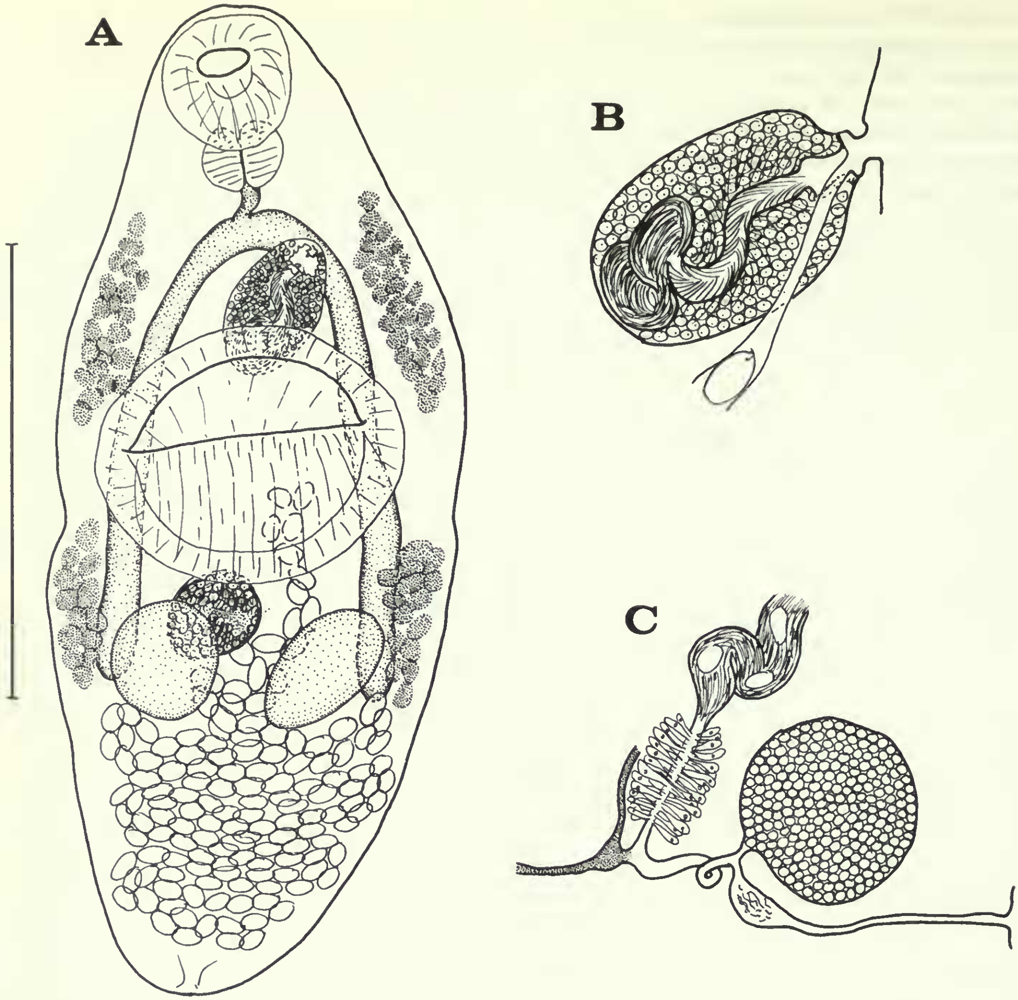

Fig. 11 *Steringotrema divergens:* (a) whole-mount specimen from *Blennius ocellaris*; (b) cirrus-sac; (c) diagram of female proximal genitalia. Bar scale: a = 0.5 mm.

specimens. The worm is of an elongate oval shape, sometimes showing a slight 'waist' at the level of the ventral sucker (Fig. 11a). The tegument is unarmed. The dimensions of this worm are given in Table 8. The globular, subterminal *oral sucker* is usually at most half the size of the larger, globular *ventral sucker*, which is situated just anterior to the middle of the body. There is a short prepharynx, which leads into a well-developed, globular *pharynx*. The oesophagus is short, bifurcating at about the level of the genital pore and giving rise to the two gut-caeca which reach back to about the level of the posterior margin of the testes.

The terminal *excretory pore* leads into a 'V'-shaped vesicle, the arms of which reach forward dorso-laterally to the level of the pharynx.

The oval *testes* lie close to the posterior margin of the ventral sucker in a symmetrical formation. The vasa efferentia pass separately, but close together, through the wall of the cirrus-sac. The *cirrus-sac* is broadly oval and may just overlap the ventral sucker posteriorly (Fig. 11a & b). It contains a bipartite, saccular seminal vesicle, a recurved and narrow pars prostatica with a filamentous lining, and a wide and diverticulate ejaculatory duct. In some specimens the seminal vesicle is empty and forms a simple tube. The genital atrium is quite small and opens ventrally through the genital pore just to the left of the median line in about the middle of the forebody.

The subglobular *ovary* lies anteriorly or antero-medially to the right testis. From its ventral surface the oviduct arises and passes ventrally following a convoluted course. Almost immediately after leaving the ovary it receives Laurer's canal, which may be slightly dilate proximally and contain a few spermatozoa. Laurer's canal opens dorsally at about the level of the posterior margin of the ovary (Fig. 11c). Just prior to entering a weakly developed Mehlis' gland which lies ventrally to the ovary, the oviduct receives the common vitelline duct. The proximal region of the *uterus* forms a uterine seminal receptacle. The majority of the remainder of the uterus, which contains numerous operculate and smooth-shelled eggs, is coiled in the post-testicular region of the hindbody, but a narrow section passes anteriorly between the testes and opens into the genital atrium from the left side via a narrow, muscular metraterm. The follicular *vitellarium* is disposed in four small groups laterally and symmetrically, two in the forebody and two in the anterior hindbody. The fields in the forebody reach from the level of the pharynx or the intestinal bifurcation to the level of the anterior third of the ventral sucker, and the fields in the hindbody extend from the level of the posterior margin of the ventral sucker to about the level of the posterior margin of the testes. The main lateral vitelline ducts unite ventrally to the ovary to form a short common vitelline duct, which is slightly dilate and thus forms a small vitelline reservoir prior to uniting with the oviduct (Fig. 11c).

Table 8 Dimensions of *Steringotrema divergens* from the present material and from the literature

Authority	Mathias (1934)	Bray (1973)	Lopez-Roman & Guevara-Pozo (1974)	Present material
Host	*Blennius ocellaris*	*Capros aper*	*Blennius ocellaris*	*Blennius ocellaris*
Locality	Banyuls	Bay of Biscay & Morocco	Spain	Plymouth
Length (mm)	0·97–2·0	0·75–1·2	1·6–1·75	0·92–1·14
Breadth (mm)	0·5–1·0	0·42–0·47	0·72–0·79	0·44–0·48
Length : forebody ratio	(1 : 0·41)	1 : 0·20–0·42*	(1 : 0·38)	1 : 0·29–0·40
Oral sucker (mm)	0·15–0·20	0·11–0·15 dia.	0·16–0·21 × 0·195–0·26	0·12–0·16 × 0·14–0·16
Ventral sucker (mm)	0·28–0·40 × 0·35–0·48	0·21–0·31 × 0·38–0·42	0·36–0·41 × 0·40–0·45	0·26–0·30 × 0·32–0·38
Sucker ratio	(1 : 2·3)	1 : 2·7–3·6	(1 : 2·2)	1 : 2·0–2·7
Pharynx (mm)	0·10–0·15	0·9–0·11 dia.	0·12–0·14 × 0·15–0·18	0·10–0·12 dia.
Oesophagus (mm)	–	–	–	about 0·12–0·19
Cirrus-sac (mm)	0·20–0·30 × 0·15–0·20	0·18–0·19 × 0·11–0·13	(0·29 × 0·15)	0·19 × 0·13
Testes (mm)	0·13–0·18 × 0·18–0·28	–	0·13–0·195 × 0·12–0·15	0·13–0·17 × 0·11–0·13
Ovary (mm)	0·10–0·17 × 0·10–0·19	–	0·105–0·13 × 0·074	0·08–0·13 × 0·09–0·10
Eggs (μm)	40–55 × 22–32	46–48 × 33–37	47–49 × 30–33	44–55 × 28–36

* New data.

DISCUSSION. The unique vitelline distribution of this worm sets it apart from other species of the genus. Nicoll (1914) described the ovary as being indistinctly trilobate, but most descriptions and our own material indicate that the ovary is normally more or less globular, although it may have slightly indented margins. Palombi (1931*a*) described and figured a seminal receptacle. This appears to be the slightly dilate part of Laurer's canal that we have observed, which may contain small numbers of, presumably, spent spermatozoa. As a uterine seminal receptacle is present, this is unlikely to actually function as a seminal receptacle. It is probably identical to the structure which we have referred to as a 'rudimentary seminal receptacle' in hemiuroids (Gibson & Bray, 1977: 168; 1979: 50).

Steringotrema ovacutum (Lebour, 1908) Yamaguti, 1953

Steringophorus ovacutus Lebour, 1908.
Rhodotrema ovacutum (Lebour) Odhner, 1911.
Stenakron ovacutus (Lebour) Strelkov, 1960.

TYPE-HOST AND LOCALITY. *Hippoglossoides platessoides*, Northumberland coast, England.

RECORDS
(i) Material studied
(a) From NE Atlantic

Mature worms
Hippoglossoides platessoides [intestine] Cullercoats, Northumberland, England (May, 1972). Material of J. Thulin.

Immature worms
Hippoglossoides platessoides [intestine] Aberdeen, Scotland (Oct., 1973) BM(NH) 1977.5.25.7.
Lycodes vahli [intestine] Kristineberg, Sweden (Dec., 1971). Material of J. Thulin.

(b) From elsewhere

Mature worms
Hippoglossoides platessoides [intestine] Newfoundland and Nova Scotia (see Bray, 1979 : 420). BM(NH) 1977.2.16.57–64.

Immature worms
Anarhichas lupus [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.56.
Hippoglossoides platessoides [intestine] Newfoundland and Labrador (see Bray, 1979 : 420). BM(NH) 1977.2.16.57–64.
Lycodes vahli [intestine] Newfoundland (see Bray, 1979 : 420). BM(NH) 1977.2.16.65.

(ii) NE Atlantic records from the literature
Hippoglossoides platessoides [intestine] Northumberland coast, England (June, Nov., 1907). Lebour (1908*a* : 35; 1908*b* : 42; as *Steringophorus ovacutus*).
—— [intestine] Kristineberg, Sweden. Odhner (1911*a* : 100; as *Rhodotrema ovacutum*).
– [intestine] Aberdeen, Scotland. Nicoll (1913 : 190; as *Rhodotrema ovacutum*).

ASPECTS OF BIOLOGY. The life-history of this parasite is not known, although Scott (1975*a*), after having noted that the incidence of the worm in *Hippoglossoides platessoides* of various sizes paralleled that of the incidence of sea-urchins and sand-dollars in their food, suggested that these particular animals 'merited investigation as potential intermediate hosts'.

All of our adult worms came from the long-rough dab (*H. platessoides*), and prior to this work it was the only known host in the NE Atlantic region. It appears, however, that the worm can survive for a time, although apparently not mature, in the blennioid fishes *Lycodes vahli* and *Anarhichas lupus*. The distribution of *S. ovacutum* extends from the eastern coast of Canada across the northern North Atlantic to the Barents Sea, the Mediterranean Sea and in the northern North Pacific from the Bering Sea through the Sea of Okhotsk to the Sea of Japan. Throughout its distribution this species appears to have a definite predilection for pleuronectid hosts.

PREVIOUS DESCRIPTIONS. Lebour (1908*b* : 42; as *Steringophorus ovacutus*); Odhner (1911*a* : 100; as *Rhodotrema ovacutum*); Polyansky (1955 : 54; as *Rhodotrema ovacutum*); Skrjabin & Koval

(1957 : 250; as *Rhodotrema ovacutum*); Zhukov (1960 : 32; as *Rhodotrema ovacutum*); Mamaev *et al.* (1963 : 96; as *Rhodotrema ovacutum*).

Description (Fig. 12). Only six mature specimens were available for study, one of which was serially sectioned, and numerous immature specimens, one of which was also sectioned. The dimensions of this species are summarized in Table 9. This worm is ovoid (Fig. 12a & b) and the body-surface is smooth. There is a subterminal, globular *oral sucker*, which is normally slightly more than half the breadth of the bulky, muscular *ventral sucker*. The latter sucker is situated in the middle (in immature worms) or slightly anterior to the middle (in mature worms) of the body and possesses an aperture which is often directed anteriorly. There is a short prepharynx that leads into a well-developed globular *pharynx*. The oesophagus is also short and is surrounded by gland-cells. The intestinal bifurcation occurs between the middle of the forebody and the anterior margin of the ventral sucker (Fig. 12a & b). The usually wide caeca reach back into the hindbody to a position lateral to the testes, where they terminate blindly.

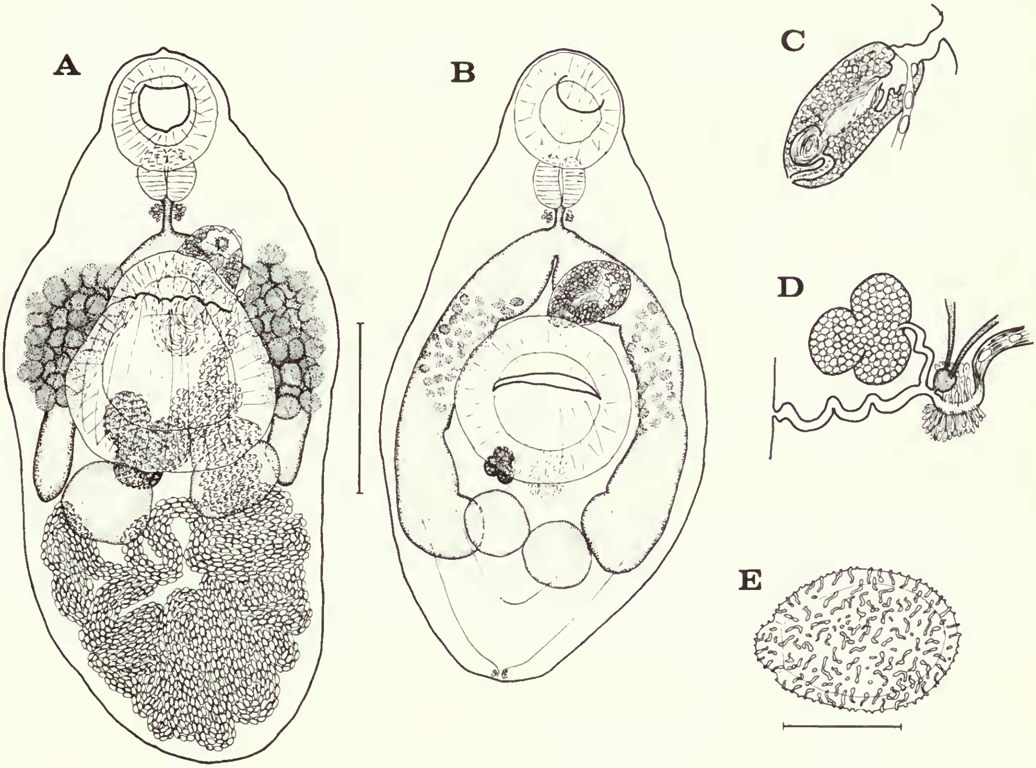

Fig. 12 *Steringotrema ovacutum:* (a) mature specimen from *Hippoglossoides platessoides:* (b) immature specimen from *Anarhichas lupus*; (c) cirrus-sac; (d) diagram of female proximal genitalia; (e) egg. Bar scale: a, b = 0·5 mm; e = 50 μm.

The *excretory pore* is terminal and leads into a 'V'-shaped vesicle with a dilate base and wide arms in the hindbody (Fig. 12b). In the forebody the arms become narrower and reach to the level of the pharynx.

The *testes* are oval to globular and are arranged more or less symmetrically close to the posterior margin of the ventral sucker in the ventral plane: the testes are especially close to the ventral sucker in mature specimens. The vasa efferentia are difficult to follow but appear to pass through the wall of the cirrus-sac close together, but separately. The *cirrus-sac* is an oval structure containing the seminal vesicle, pars prostatica and ejaculatory duct. The seminal vesicle is

Table 9 Dimensions of *Steringotrema ovacutum* from the present material and from the literature

Authority	Lebour (1908*b*)	Odhner (1911*a*)	Zhukov (1960, and in Skrjabin & Koval, 1957)	Present material
Hosts	*Hippoglossoides platessoides*	*Hippoglossoides platessoides*	*Hippoglossoides elassodon dubius*, *Cleisthenes herzensteini*	see text
Locality	Northumberland	W. Sweden	Sea of Japan	see text
Length (mm)	1·8–2·3	1·2–1·5	1·8–3·93	0·81–2·3
Breadth (mm)	1·16–1·33	0·55–0·63	1·31–2·1	0·49–1·08
Length : forebody ratio	(1 : 0·38)	(1 : 0·26)	(1 : 0·36)	1 : 0·29–0·49 (immature) 1 : 0·26–0·36 (mature)
Oral sucker (mm)	0·32–0·40 across	0·25–0·27	–	0·11–0·42 × 0·15–0·39
Ventral sucker (mm)	0·6–0·8 across	0·4–0·5	–	0·30–0·68 × 0·32–0·81
Sucker-ratio	1 : 2	(1 : 1·9)	(1 : 1·8)	1 : 1·6–2·6
Pharynx (mm)	–	0·11–0·13	–	0·10–0·22 × 0·10–0·19
Oesophagus (mm)	–	–	–	0·03–0·1
Cirrus-sac (mm)	0·3 long	–	–	0·10–0·37 × 0·10–0·22
Testes (mm)	0·12 long	–	–	0·06–0·29 × 0·06–0·27
Ovary (mm)	–	–	–	0·11–0·31 × 0·09–0·26
Eggs (μm) *	46 × 26	48 × 28	46–50 × 29–33	38–50 × 29–38

* Further egg measurements: 36–50 × 21–29 (Polyansky, 1955).

bipartite, normally consisting of two globular or short, cylindrical parts which are distended with spermatozoa (Fig. 12a); but in some specimens it may be almost empty and reduced to a narrow tube (Fig. 12c). The wide pars prostatica is almost straight and lined with filamentous projections, and the muscular wall of the ejaculatory duct has many irregular diverticula. The genital atrium is small and opens ventrally through the genital pore, which lies to the left of the median line in the posterior half of the forebody.

The trilobed *ovary* has a clover leaf-like outline, and lies dorsally to the posterior margin of the ventral sucker. It lies in a more dorsal plane than the testes, and is situated anterior or anteromedial to the right testis. The oviduct passes ventrally from the ovary, and prior to entering Mehlis' gland it receives Laurer's canal and the common vitelline duct (Fig. 12d). Laurer's canal opens dorsally at the level of the posterior margin of the ovary, after having followed a convoluted course. A uterine seminal receptacle is present. The bulk of the *uterus* lies posterior to the testes, normally filling the entire post-testicular region of the hindbody in mature specimens. The distal region of the uterus passes anteriorly dorsal to the left side of the ventral sucker, and opens into the genital atrium from the left. The numerous, operculate eggs vary considerably in size and have a distinctive type of pattern etched onto the surface of the shell (Fig. 12e). The *vitellarium* consists of two lateral fields of tightly packed follicles, which are situated symmetrically. These fields extend from a level between the intestinal bifurcation and the anterior margin of the ventral sucker to a posterior limit between the middle and the posterior margin of the ventral sucker. The follicles feed two main lateral ducts which unite to form a short common duct lying adjacent to Mehlis' gland. The common duct is distended to form a small vitelline reservoir (Fig. 12d).

Discussion. This species possesses eggs with ornamented or etched shells. This feature has also been illustrated by Mamaev *et al.* (1963); but it is surprising that it has not been commented on prior to this, especially as some of the earlier workers have obviously examined the eggs carefully. Lebour (1908*b*), for example, coined the specific name because of what she considered to be the unusual shape of the eggs. A similar ornamentation of the egg-shell probably occurs in the similar species *S. phrissovum* (Aldrich, 1961), where the eggs are described as spiny, and also in more distantly related fellodistomines, such as *Benthotrema plenum* Manter, 1934, and *Steringophorus blackeri* Bray, 1973.

This species was used by Odhner (1911*a*) to erect the genus *Rhodotrema*, which is supposed to differ from *Steringotrema* in possessing a 'Y'-shaped excretory vesicle, a shorter and more muscular pars prostatica and a less rounded cirrus-sac. The excretory vesicle is, however, practically 'V'-shaped, and the other two characters, which are open to doubt, are not criteria of importance at the generic level. There appears, therefore, to be no good reason for maintaining *Rhodotrema* as a distinct genus. The confusion between *Rhodotrema* and members of the Stenakrinae Yamaguti, 1970, which has led to a number of species (see p. 232) being erroneously placed in this genus, is probably due to Odhner's (1911*a*) figure, which is of an immature worm and gives no indication of the full uterine distribution. In the Stenakrinae the uterus is confined to the pre-testicular region. Other points of difference between the latter group and the fellodistomines are listed on p. 201.

Genus *PRUDHOEUS* gen. nov.

Definition. Body small, elongate oval. Body-surface smooth. Oral sucker globular; subterminal. Ventral sucker transversely oval; much larger than oral sucker; inside anterior half of body. Hindbody longer in mature specimens than in immature worms. Prepharynx small. Pharynx oval, well developed. Oesophagus short. Intestinal bifurcation near middle of forebody; caeca end blindly close to posterior extremity. Testes two; irregularly rounded to oval; more or less symmetrical in anterior hindbody; post-ovarian. Cirrus-sac oval; containing bipartite seminal vesicle, wide pars prostatica with external gland-cells and filamentous lining, and well-developed ejaculatory duct [wide and diverticulate in other members of subfamily]. Well-developed cirrus often present. Genital atrium present; shallow. Genital pore ventrally submedian, sinistral; at about level of intestinal bifurcation; may be wide when cirrus everted. Spermatophores may be present. Ovary trilobed; anterior to right testis or approximately median. Laurer's canal and uterine seminal receptacle present. Uterus mainly post-testicular; reaches to posterior extremity. Eggs small; operculate; without spines, filaments or ornamentation on shell. Vitellarium follicular; in two lateral fields; mainly in ventro-lateral plane; between the level of the posterior margin of ventral sucker and a level posterior to the middle of the hindbody; fields may almost unite ventrally. Excretory pore terminal; vesicle 'V'-shaped, with arms reaching into forebody. Parasitic in upper intestine of marine teleosts.

Type-species. *Prudhoeus nicholsi* sp. nov.

Comment. This new genus is probably most closely related to *Lomasoma* Manter, 1935, and *Lissoloma* Manter, 1934. It differs from the former in lacking any lateral lobation of the body, from the latter in body-shape, and from both in possessing a trilobed, rather than a multilobate, ovary, in lacking polar processes or filaments on the eggs and in having much of the vitellarium in the ventral plane.

This genus is named in honour of our colleague Mr S. Prudhoe OBE for contributions to helminth-taxonomy and the years of advice from which we have benefited.

Prudhoeus nicholsi sp. nov.

Type-host and locality. *Polyacanthonotus rissoanus*, off W of Ireland (55°N, 10°W).

Records
(i) Material studied
(a) From the NE Atlantic

Polyacanthonotus rissoanus [upper intestine] Off St Kilda, Scotland (57°N, 09°W; depth 980–1030 m; June, 1974). BM(NH) (paratype) 1977.6.14.366.

—— [upper intestine] W of Tory Island, off W of Ireland (55°N, 10°W; depth 800–825 m; June, 1974). BM(NH) (holotype) 1977.6.14.365; (paratypes) 1977.6.14.367.

—— [intestine] Flannan region, NW of Scotland (58°N, 10°W; depth 1300–1320 m; Oct., 1978). BM(NH) 1979.2.14.7–11 (paratypes).

ASPECTS OF BIOLOGY. According to Wheeler, in Hureau & Monod (1973), *Polyacanthonotus rissoanus*, the host of this species, is benthic, occurring in deep waters of the Mediterranean and eastern Atlantic off Morocco. Our observations indicate that this fish also occurs on the edge of the continental shelf further to the north. It appears that, like *Steringophorus pritchardae* and *Olssonium turneri*, this species is a deep-water form. It appears that spermatophores are used in sperm-transfer.

PREVIOUS DESCRIPTIONS. None.

DESCRIPTION (Fig. 13). Fifteen worms were found, two of which were serially sectioned. Three of the worms are in an early mature condition (Fig. 13b). The larger adult worms are elongate oval, and it is apparent that the hindbody increases in size relative to the forebody at a much faster rate as the worm grows (cf. Figs 13a & b). The body-surface is smooth, and the sub-tegumentary parenchyma contains many gland-cells. The body-length varies between 1·24 and 2·90 mm and the maximum width between 0·37 and 0·86 mm. The forebody, which tapers sharply, is less than a quarter (0·17–0·22) of the body-length in the largest specimens, but a much greater

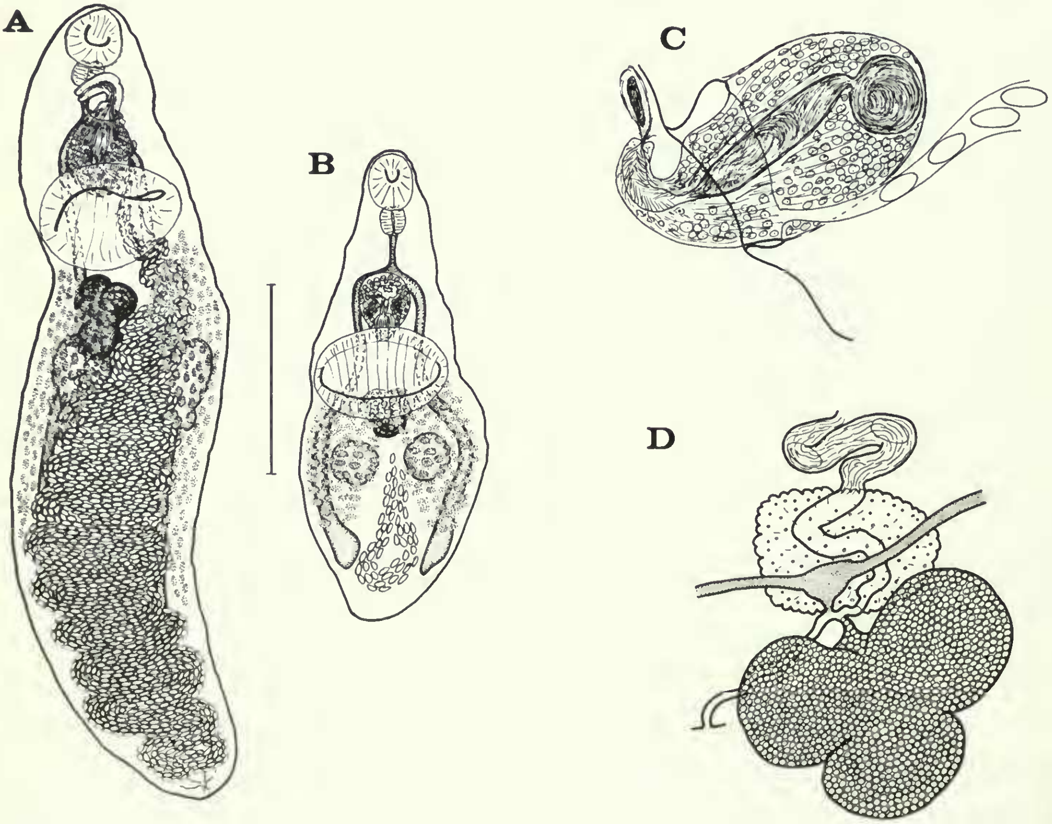

Fig. 13 *Prudhoeus nicholsi:* (a) large specimen, ventral view; (b) small specimen, ventral view; (c) cirrus-sac; (d) diagram of female proximal genitalia. Bar scale: a, b = 0·5 mm.

proportion (0·26–0·37) of the body-length in the smaller specimens. The hindbody, when filled with the voluminous uterus, has roughly parallel sides with a rounded or slightly indented posterior margin, but in the smallest specimen it is broadly oval. The subglobular, subterminal *oral sucker* (0·11–0·20 × 0·10–0·17 mm) is smaller than the transversely oval *ventral sucker* (0·23–0·40 × 0·26–0·43), the ratio being 1 : 2·3–3·7. The aperture of the ventral sucker may be directed anteriorly. There is a very short prepharynx, which leads into a globular *pharynx*, measuring about 0·064–0·09 mm in diameter. The short oesophagus (0·05–0·10 mm in length) bifurcates at about the middle of the forebody, and the caeca, which are narrow and straight, reach into the posterior half of the post-testicular zone, where they end blindly.

The *excretory pore* is terminal and leads into a short, narrow glandular duct which leads into a 'V'-shaped vesicle. The arms reach dorso-laterally into the forebody to the level of the cirrus-sac.

The irregularly rounded to oval *testes* (0·16–0·29 × 0·08–0·19 mm) lie symmetrically or slightly obliquely in the anterior hindbody. The vasa efferentia pass close together, but separately through the wall of the cirrus-sac. The *cirrus-sac* (0·16–0·24 × 0·12–0·20 mm) lies in the posterior forebody, slightly overlapping dorsally the anterior margin of the ventral sucker. It is globular to oval, and contains a bipartite seminal vesicle, a wide pars prostatica with external gland-cells and filamentous lining and an ejaculatory duct. The proximal region of the seminal vesicle is globular and the distal region is oval. In two of our specimens, including the sectioned specimen, the cirrus is everted, thus modifying the normal arrangement of the contents of the cirrus-sac. The pars prostatica is typical of the subfamily, but in the everted specimens it is pushed forward into the cirrus (Fig. 13c): this movement may also be partly responsible for the elongate oval shape of the distal part of the seminal vesicle. The ejaculatory duct of the everted specimens forms the outer wall of the cirrus. When the cirrus is withdrawn the ejaculatory duct is wide and diverticulate, as it is in other fellodistomines. When everted the cirrus is a large conical structure which extends through the genital pore. In the sectioned specimen a spermatophore can be seen lying close to the end of the cirrus. The genital atrium appears to be shallow, although like the genital pore, which is situated just to the left of the median line at about the level of the intestinal bifurcation, it appears to be wide when the cirrus is everted.

The trilobed *ovary* (0·16–0·26 × 0·13–0·24 mm) lies antero-medially to the right testis, or in the median line, close to the posterior margin of the ventral sucker. The short oviduct passes antero-ventrally from the ovary to Mehlis' gland. Prior to its entry into Mehlis' gland it receives Laurer's canal and the common vitelline duct (Fig. 13d). Laurer's canal passes over the posterior surface of the ovary and opens dorsally at the level of the testes. A uterine seminal receptacle is present, formed by the initial loops of the *uterus*, the majority of which is coiled in the post-testicular zone. The loops of the uterus extend from the posterior end of the body forward through the intertesticular region to the level of the ovary and a single uterine sling reaches anteriorly towards the genital atrium into which it opens to the left of the cirrus-sac. The numerous, operculate eggs (36–44 × 21–25 μm) lack spines, filaments or ornamentation on the shells. The *vitellarium* is follicular, lying in two lateral fields reaching from the level of the posterior margin of the ventral sucker to just inside the posterior half of the hindbody. The follicles lie mainly in the ventral parenchyma, but pass laterally to the caeca and just into the dorsal field. In the anterior region of the hindbody the vitelline fields come close together ventrally as they are wider in this region. The main lateral vitelline ducts unite ventrally to Mehlis' gland to form the common vitelline duct, which is enlarged proximally to form a distinct vitelline reservoir.

DISCUSSION. Probably the most similar species to *P. nicholsi* in our region is *Steringophorus furciger*. The two can, however, easily be distinguished by the shape of the excretory vesicle, the shape of the ovary, the length of the caeca and the distribution of the vitellarium. This species is also similar to *Steringotrema* sp. of Armstrong (1974) from the macrourid *Ventrifossa atlantica* in the eastern Gulf of Mexico. The sucker-ratio of this unnamed species is smaller ['1 : 1·8–2·2 (2·8 in one specimen)']. The supposed claviform nature of the seminal vesicle and the absence of Laurer's canal also serve to differentiate it from *P. nicholsi*.

This species is named in honour of Mr John H. Nichols of the MAFF Laboratory, Lowestoft, for his help to one of us (R. A. B.) on numerous occasions.

Subfamily **BACCIGERINAE** Yamaguti, 1958

Pentagramminae Yamaguti, 1958.

DIAGNOSTIC FEATURES. Body small; oval to fusiform. Body-surface smooth or finely spined. Oral sucker subterminal; smaller to larger than ventral sucker. Ventral sucker in middle or anterior half of body. Prepharynx short. Pharynx small; globular to oval. Oesophagus distinct; short to long. Intestinal bifurcation in forebody. Caeca reaching to testicular region or just beyond. Testes two; symmetrical to slightly oblique; in anterior hindbody. Cirrus-sac thin-walled or occasionally absent. Seminal vesicle bipartite; large; enclosed in cirrus sac when latter present. Pars prostatica apparently absent or short; tubular with few external gland-cells. Ejaculatory duct short, narrow; may evert to form small cirrus. Genital atrium deep, narrow. Genital pore median or submedian in posterior forebody. Ovary oval to lobed; inter- or post-testicular. Laurer's canal present; long, opening at or near posterior extremity; proximal region dilated to form canalicular seminal receptacle. Uterine seminal receptacle absent. Uterus almost entirely post-testicular; extensive; opens into genital atrium at base of cirrus-sac. Eggs numerous; small; operculate; shells smooth, without spines or filaments. Vitellarium in two fields, each with one or several compact clusters of small follicles; fields symmetrical in lateral regions of forebody or anterior hindbody; vitelline ducts wide, conspicuous. Excretory vesicle 'Y'-shaped, with short stem (in fact almost 'V'-shaped); arms reach into forebody. Parasitic in intestine and stomach of marine and brackish water teleosts.

COMMENT. Yamaguti (1958) erected the Baccigerinae for *Bacciger* Nicoll, 1914, as a subfamily of the Cryptogonimidae Ward, 1917, and the Pentagramminae for *Pentagramma* Chulkova, 1939, as a subfamily of the Fellodistomidae. He later (1971) considered the Baccigerinae to be a fellodistomid subfamily, containing *Bacciger*, *Faustula* Poche, 1926, *Pseudobacciger* Nahhas & Cable, 1964, and *Pseudopentagramma* Yamaguti, 1971 (a replacement name for the pre-occupied *Pentagramma*). We agree with his later work, as far as the genera *Bacciger* and *Pseudopentagramma* (which we call *Pronopryma* – see below) are concerned, considering them to be morphologically similar enough to be placed in the same subfamily. The structure of the contents of the cirrus-sac and the proximal part of the female reproductive system are especially similar in these two genera. They have not generally been considered to be closely related, however, although *Bacciger* was originally placed in the Fellodistomidae and *Pentagramma* in the Steringophoridae. Yamaguti (1938, 1953) considered *Bacciger* to be a heterophyid, and, as mentioned above, in 1958 he considered it a cryptogonimid. Baer & Joyeux (1961) listed *Bacciger* as a cryptogonimine and *Pentagramma* as a fellodistomine. A detailed taxonomic history of the two genera was presented by Margolis & Ching (1965), and they pointed out that, despite Yamaguti's views at that time, Manter (1947) had retained *Bacciger* in the Fellodistomidae on the basis of the presence of a cirrus-sac. Mehra (1963) also considered *Bacciger* a fellodistomid, pointing out that its life-history is most dissimilar to that of the cryptogonimids. With regard to the Pentagramminae Mehra (1963) considered it synonymous with the Antorchiinae Yamaguti, 1958 [*sic*]. The Antorchiinae Skrjabin & Koval, 1957 (syn. Parantorchiinae Yamaguti, 1958 – see Machida, 1975) certainly contains species similar to those of the Baccigerinae, suggesting strongly that the relationship between these subfamilies is worth further study. A few differences are, however, apparent: these include the nature of the contents of the cirrus-sac and both the presence of dorsal pouches and the presence of the gonads in the forebody in the Antorchiinae. In the present work *Faustula* (syn. *Orientophorus* Srivastava, 1935) is not considered to be a member of the Baccigerinae, as it apparently differs in the shape of the seminal vesicle, the nature of the vitellarium and the presence of a deeply multilobate ovary. If further study indicates that a wider concept of the Baccigerinae including the Antorchiinae is appropriate, then *Faustula* would comfortably fit into such a concept.

The Baccigerinae is probably one of the most aberrant of the fellodistomid groups, having a canalicular seminal receptacle, a long, narrow genital atrium and often fine spines on the body-surface. In addition, it sometimes lacks a cirrus-sac. The spines, when present, are apparently easily lost or not seen, and are probably not similar in construction to those of such prominently spined groups as the zoogonids or lepocreadiids. They are too small to be studied satisfactorily by light microscopy, but, as yet, no studies have been carried out on the species of this group using more critical techniques.

Key to the genera of the Baccigerinae recorded from the northeast Atlantic

1 Body-surface covered with minute spines; body oval; cirrus-sac globular; papilla-like cirrus normally present; ovary intertesticular; Laurer's canal opens at posterior extremity; vitellarium 3 to 4 clusters of follicles in each lateral field, normally in forebody ***BACCIGER*** Nicoll, 1914 (p. 249)

– Body-surface smooth; body fusiform; cirrus-sac elongate; cirrus not normally present; ovary post-testicular; Laurer's canal opens on dorsal surface close to posterior extremity; vitellarium one cluster of small follicles in each lateral field, in hindbody ***PRONOPRYMNA*** Poche, 1926 (p. 254)

Genus *BACCIGER* Nicoll, 1914

(?) *Ovotrema* Pigulewsky, 1938.

DIAGNOSTIC FEATURES. Body small, oval. Body-surface covered with small spines, which are easily lost or overlooked. Cirrus-sac present; oval; well developed, but with thin wall; dorsal or antero-dorsal to ventral sucker. Seminal vesicle internal; large; bipartite. Pars prostatica short; surrounded by few gland-cells. Ejaculatory duct narrow. Cirrus normally papilla-like. Ovary oval to lobed; usually more or less inter-testicular. Laurer's canal long, narrow; opening at posterior extremity and dorsally to excretory pore. Canalicular seminal receptacle present. Vitellarium two symmetrical fields of a few clusters or masses of small follicles (these clusters may break up); lateral to ventral sucker and/or in forebody. Parasitic in stomach or intestine of marine or brackish water teleosts.

TYPE-SPECIES. *Bacciger bacciger* (Rudolphi, 1819) (by monotypy).

COMMENT. Only a single species of *Bacciger*, the type-species, has been recorded in our region. As the other species of the genus are not well known with regard to their detailed morphology, our conception of its diagnostic features are based mainly upon this species.

Of the nine species which have been assigned to this genus, we consider that there are only four which are probably valid. These are:

(1) *Bacciger bacciger* (Rudolphi, 1819) Nicoll, 1914; type-species of the genus (p. 250).

(2) *B. cochinensis* Hafeezullah & Siddiqi, 1970; from the intestine of *Thrissocles mystax* off India.

(3) *B. grandispinatus* Naidenova, 1970; from the intestine of *Mesogobius batrachocephalus* in the Azov Sea.

(4) *B. ovatus* (Price, 1934) comb. nov. [syns. *Steringotrema ovata* Price, 1934, *Fellodistomum ovatum* (Price) Yamaguti, 1971, *B. opisthonemae* Nahhas & Cable, 1964]; this species was first described from a single specimen from the pyloric caeca of *Opisthonema oglinum* off Puerto Rico. Nahhas & Cable (1964) described their new form, *B. opisthonemae*, from the caeca of the same host off Jamaica. As Nahhas & Cable pointed out, the two descriptions differ only slightly, and we believe that there can be little doubt that the two worms are conspecific. Price failed to see spines on the tegument; but these are frequently lost or overlooked in this genus. The different configurations of the testes and ovary are probably explained by flattening or misinterpretation. This species differs from other species of *Bacciger* in having longer caeca, and a genital pore which is submedian and much more anteriorly positioned.

The remaining five species are:

(1) *Bacciger harengulae* Yamaguti, 1938; this species was used as the type-species of the genus *Pseudobacciger* by Nahhas & Cable (1964).

(2) *B. melanostomum* Naidenova, 1970; from the intestine of *Neogobius melanostomus* in the Azov Sea. This species differs from *Bacciger* in having a pre-testicular uterus and a continuous band of vitelline follicles across the anterior hindbody. It has been suggested to us by Dr A. V. Gaevskaja (*in litt.*) that this species corresponds to '*Pentagramma*' *petrowi* (Layman, 1930) which occurs in the same host.

(3) *B. nicolli* Palombi, 1934; a synonym of *B. bacciger* (see p. 253).

(4) *B. petrowi* (Layman, 1930) Zhukov, 1959; now considered to be a species of *Pronoprymna* (see p. 259).
(5) *B. sardinellae* Hafeezullah & Siddiqi, 1970; from the intestine of *Sardinella fimbriata*, India. This species is possibly a member of the genus *Pronoprymna*.

Bacciger bacciger* (Rudolphi, 1819) Nicoll, 1914

Distoma baccigerum Rudolphi, 1819.
Distoma (*Dicrocoelium*) *baccigerum* (Rudolphi) Parona, 1912.
Dicrocoelium baccigerum (Rudolphi) Zernov, 1913.
(?) *Cercaria lata* Lespés, 1857.
(?) *Cercaria pectinata* Huet, 1891.
(?) *Cercaria lutea* (van Beneden) of Giard (1897).
Bacciger nicolli Palombi, 1934.
Pseudobacciger nicolli (Palombi) Yamaguti, 1971.
(?) *Ovotrema pontica* Pigulewsky, 1938.
(?) *Steringotrema* (*Ovotrema*) *ponticum* (Pigulewsky) Yamaguti, 1953.

TYPE-HOST AND LOCALITY. *Atherina hepsetus*, Naples, Italy.

RECORDS
(i) Material studied
(a) From the NE Atlantic
Atherina presbyter [stomach] Loch Maddy, North Uist, Outer Hebrides, Scotland (Nov., 1952) (see Margolis & Ching, 1965; as *B. nicolli*). Material lent by L. Margolis.
—— [stomach] Port Erin, Isle of Man, Irish Sea (July, 1960). BM(NH) 1977.9.30.2–7.
—— [stomach] Salcombe, Devon, England (Nov., 1967). BM(NH) 1977.9.30.1.
—— ['gut'] Solent, Hampshire, England. Collected by T. Reader. BM(NH) 1979.2.14.23.

(b) From elsewhere
None

(ii) NE Atlantic records from the literature
Atherina presbyter [stomach] North Uist, Outer Hebrides, Scotland (Nov., 1952). Margolis & Ching (1965 : 388; as *B. nicolli*).
—— [stomach] Plymouth, Devon, England. Nicoll (1914 : 481).

ASPECTS OF BIOLOGY. Records of the intra-molluscan stages, including cercariae, from the NE Atlantic region which are claimed to belong to *B. bacciger* are as follows:
Barnea candida. Boulogne, Artois, France. Giard (1897 : 954; as *Cercaria lutea*). Wimereux, Artois, France. Pelseneer (1906 : 163; 1926 : 39; as *Cercaria pectinata* (*lutea*)).
Donax trunculus. Wimereux, Artois, France. Pelseneer (1906 : 163; as *Cercaria pectinata*).
Donax vittatus. Wimereux, Artois, France. Giard (1897 : 95; as *Cercaria lutea*); Dollfus (1925 : 59; as *Cercaria pectinata*); Pelseneer (1926 : 33; as *Cercaria pectinata*).
—— St Efflam, Finistère, France. Matricon-Gondran (1971 : 319).
—— Burry Inlet, South Wales. James *et al.* (1977 : 13; as *Cercaria pectinata*).
Venerupis decussata. Saint Vaast-la-Hougue, Manche, France. Dollfus (1925 : 59; as *Cercaria pectinata*).
Venerupis pullastra. Arcachon, Gironde, France. Jobert (1894: 519; see Pelseneer, 1906; 13; as *Cercaria pectinata*).
—— Wimereux, Artois, France. Pelseneer (1906 : 163; as *Cercaria pectinata*).
—— Saint Vaast-la-Hougue, Manche, France. Dollfus (1925 : 59; as *Cercaria pectinata*).

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* In using the specific name *bacciger*, rather than the original *baccigerum*, Nicoll (1914) appears to have treated it as an adjective and made it masculine. It is possible that the name is a lapsus for 'baccifer', meaning 'bearing berries', and might have referred to the follicular vitellarium which would have been visible to Rudolphi in uncleared specimens.

In addition to the authors listed above, the larval stages of what is thought to be *B. bacciger* have been extensively studied by Huet (1891), Palombi (1932; 1933; 1934*a*; 1934*b*; 1940), Dolgikh (1963; 1965*a*; 1966*a*; 1966*b*; 1968*a*; 1968*b*; 1970), Matricon-Gondran (1965; 1966) and Gaevskaja [née Dolgikh] (1972). The miracidium evidently enters the bivalve molluscan host, where it develops into a slender mother-sporocyst. This gives rise to a daughter-sporocyst (Yamaguti, 1975), within which the cercariae develop. The cercariae are gymnocephalous and possess both a setiferous tail and a spinulate body-surface. The metacercaria has been found in the amphipod *Erichthonius difformis*, within a thick-walled cyst, and has also been discovered still within the amphipod in the gut of *Atherina* spp. Whether all of the above records from molluscs are of *B. bacciger* is difficult, or impossible, to determine, at the present time; but the variety of bivalve genera represented among the hosts and the morphological similarity of the adults of many of the fellodistomids suggests that some confusion with other species, and especially with *Pronoprymna*, might have occurred. '*Cercaria pectinata*' has been studied in Korea by Chun & Lee (1976) and Bae, Kang & Kim (1977), but the latter authors appear to consider it to be a larval stage of *Bacciger harengulae*.

All of the records of the adult parasite from the NE Atlantic have been from *Atherina presbyter*; but elsewhere this species has been recorded in other species of *Atherina* and is also reported to occur in *Clupeonella*, *Boops*, *Sardina*, *Lutjanus*, *Sardinella*, *Engraulis* and *Alosa*, although some of these reports are questionable. Its distribution appears to follow that of *Atherina*, occurring in coastal waters in the NE Atlantic region from Britain south to North Africa, in the Mediterranean Sea and in the Black Sea. In addition, it has been recorded in the Red Sea (Parukhin, 1975, 1976).

PREVIOUS DESCRIPTIONS. Stossich (1888 : 101; 1889 : 27; as *Distomum baccigerum*); Nicoll (1914 : 481); Palombi (1933 : 1; 1934*a* : 438); Skrjabin & Koval (1957 : 193); Nikolaeva (1963 : 410); Margolis & Ching (1965 : 384; as *B. nicolli*).

DESCRIPTION (Fig. 14). Unfortunately, all but one of the specimens studied, 39 whole-mounts and 3 sets of serial sections, were taken from preserved fish, so that their condition, whilst adequate for description, was not good. The small, oval worm (Fig. 14a & b) bears, over its surface, small spines which are easily lost. The dimensions of this species are included in Table 10. The subterminal *oral sucker* is similar in size to the small and weakly developed *ventral sucker*, which lies just within the anterior half of the body. There is a short prepharynx, a globular and small *pharynx* and a distinct oesophagus of variable length. The intestinal bifurcation occurs just anteriorly to the anterior margin of the ventral sucker, and the short and narrow caeca normally reach back only to the anterior margins of the testes, although they occasionally do not reach the testes or reach back to the middle of these organs (Fig. 14a & b).

The *excretory pore* is terminal, and leads into a narrow, 'Y'-shaped vesicle which possesses a very short stem, so that in fact the vesicle is more or less 'V'-shaped. (We have referred to it as 'Y'-shaped in the Baccigerinae, although the stem is hardly any longer than in the cases of *Prudhoeus* and *Steringotrema*, which we have referred to as 'V'-shaped; but in the latter cases the arms are broad and as such reduce the size of the stem to insignificance as far as the total volume of the vesicle is concerned.) The narrow arms reach just into the forebody.

The *testes* are large, globular and symmetrical or almost symmetrical, lying immediately posterior or postero-lateral to the ventral sucker. The vasa efferentia pass through the muscular wall of the cirrus-sac separately but close together. The *cirrus-sac*, is broadly oval and occurs dorsally or dorso-laterally to the ventral sucker. It contains a large, bipartite seminal vesicle (Fig. 14c), a short and wide pars prostatica with few external gland-cells and a smooth lining, and a short and narrow ejaculatory duct which passes through a distinct, papilla-like cirrus. The cirrus is present in all of our sectioned specimens and lies at the base of a deep, narrow genital atrium, which opens in the median line almost immediately anterior to the anterior margin of the ventral sucker.

The *ovary* is irregularly oval, lying between the testes and either just posterior to or dorsal to the ventral sucker. The oviduct passes from the posterior margin and is almost immediately united with Laurer's canal (Fig. 14d). The latter canal is wide proximally and then becomes

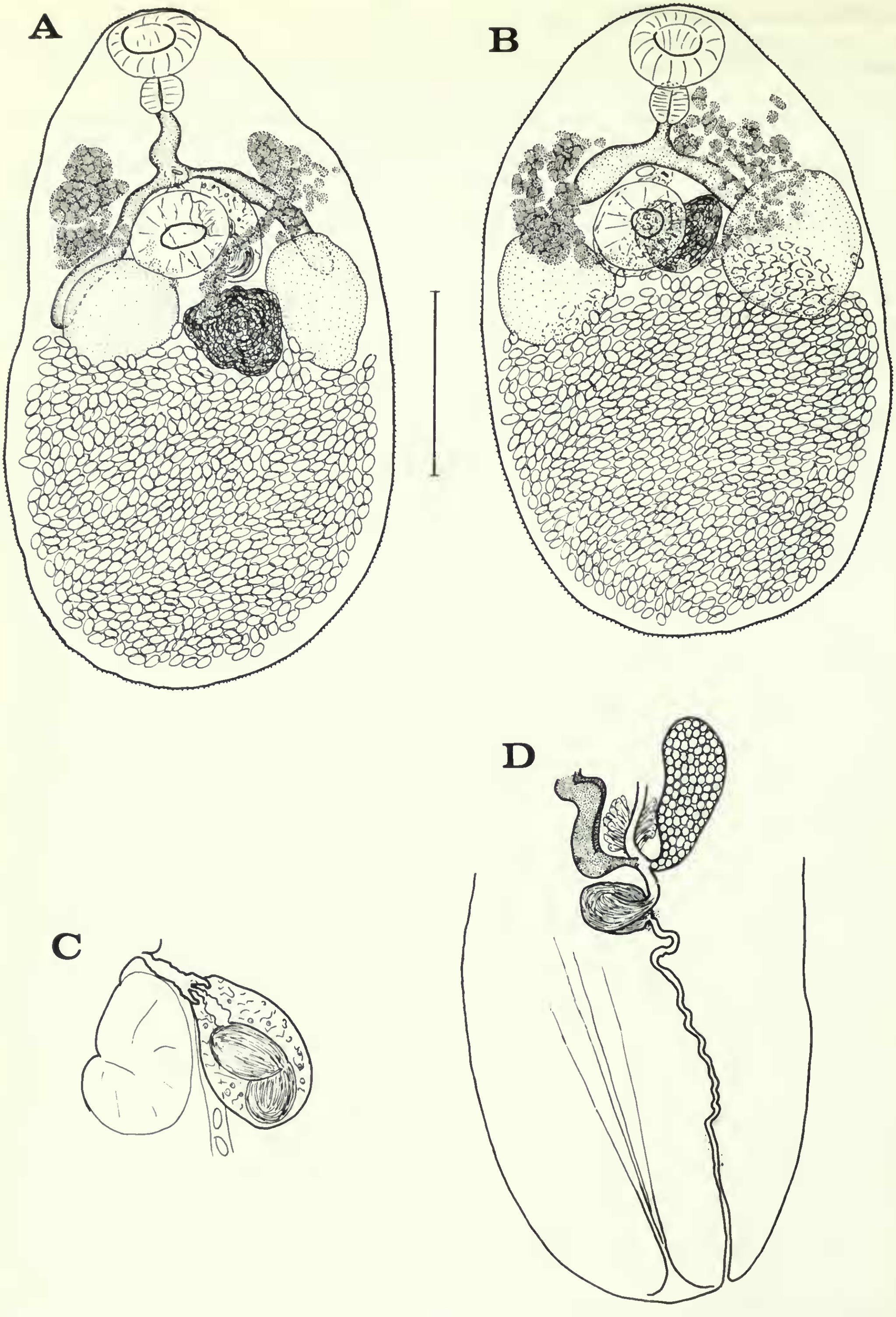

Fig. 14 *Bacciger bacciger:* (a) specimen from Salcome; (b) specimen from Port Erin; (c) cirrus-sac; (d) diagram of proximal female genitalia and part of excretory system. Bar scale: a, b = 0·2 mm.

Table 10 Dimensions of *Bacciger bacciger* from the present material and from the literature

Authority	Margolis & Ching (1965)	Margolis & Ching (1965)	Present material	Present material	Present material
Name used	*Bacciger bacciger*	*Bacciger nicolli*	*Bacciger bacciger*	*Bacciger bacciger*	*Bacciger bacciger*
Host	*Atherina hepsetus* *A. boyeri*	*Atherina presbyter*	*Atherina presbyter*	*Atherina presbyter*	*Atherina presbyter*
Locality	Black Sea, Naples	Outer Hebrides	Salcombe	Isle of Man	Solent
Length (mm)	0·59–0·90	0·72–1·08	0·81	0·48–0·64	0·87
Breadth (mm)	0·31–0·54	0·47–0·57	0·46	0·36–0·43	0·48
Length : forebody ratio	(1 : 0·26)	(1 : 0·29)	1 : 0·27	1 : 0·24–0·36	1 : 0·32
Oral sucker (mm)	0·071–0·13	0·10–0·13	0·11 × 0·75	0·087–0·105 × 0·070–0·075	0·07 × 0·11
Ventral sucker (mm)	0·066–0·097 × 0·11–0·13	0·13–0·15	0·115–0·10	0·095–0·13 × 0·090–0·094	0·13 × 0·12
Sucker-ratio	1 : 0·83–1·46	1 : 1·05–1·42	1 : 1·05	1 : 0·9–1·48	1 : 1·1
Pharynx (mm)	0·032–0·049 × 0·038–0·055	0·039–0·058	0·045 × 0·055	0·037–0·040 × 0·037–0·045	0·044 × 0·048
Oesophagus (mm)	0·065–0·12	0·039–0·097	0·065	0·060–0·082	–
Cirrus-sac (mm)	0·071–0·17 × 0·052–0·13	0·097–0·13 × 0·075–0·091	0·155 × 0·10	0·155 × 0·085	–
Testes (mm)	0·084–0·21	0·11–0·23	0·115–0·155 × 0·095–0·140	0·160–0·165 × 0·125	0·18–0·21 × 0·18
Ovary (mm)	0·10–0·15	0·10–0·17 × 0·074–0·17	0·105 × 0·095	0·10 × 0·13	0·13 × 0·14
Eggs (μm)	20–26 × 12–17	21–27 × 13–17	24–27 × 15–16	23–27 × 15–17	22–24 × 16–20

extremely wide just posterior to Mehlis' gland where it forms a large canalicular seminal receptacle. The distal extremity is delimited by a sphincter from which Laurer's canal, now narrow and convoluted, continues posteriorly through the middle of the uterine coils, and opens at the posterior extremity of the body just dorsally to the excretory pore (Fig. 14d). The distal region of the canal is almost straight. After receiving Laurer's canal the oviduct receives the common vitelline duct prior to passing through Mehlis' gland, which lies ventrally to the ovary. There is no uterine seminal receptacle. The *uterus* occupies much of the hindbody and almost the entire post-gonadal region and contains numerous operculate eggs. It is difficult to distinguish how the coils lie, but the distal region of the uterus passes anteriorly between the testes and unites with the base of the genital atrium beside the cirrus. The *vitellarium* is follicular, occurring in two lateral fields which lie between the level of the pharynx and the level of the posterior margin of the ventral sucker. The normal arrangement is apparently for the small follicles to clump together in three or four distinct masses (Fig. 14a); but in most of our material these masses have broken down and the individual follicles are scattered around the area (Fig. 14b). The vitellarium feeds two wide lateral collecting ducts which pass postero-medially towards the ovary, ventral to which they unite to form the common vitelline duct. This short duct is dilate proximally, forming a small vitelline reservoir. The lateral vitelline ducts are usually a prominent feature in the preserved worm.

DISCUSSION. The specimens described by Nicoll (1914) from Plymouth were considered by Palombi (1934*a*) to belong to a species distinct from *Bacciger bacciger* as it is known in the Mediterranean and Black Seas, and the name *B. nicolli* was given to it. Margolis & Ching (1965) record the only other previous finding of this species in the northeast Atlantic, and describe worms which are much closer to *B. bacciger* than Nicoll's description. They argue, however, that the northeastern Atlantic form (*B. nicolli*) is distinct from *B. bacciger* on two grounds: (1) they point out that it has been found only in the stomach of *Atherina presbyter*, whilst the Mediterranean/Black Sea form is only found in the intestine of its hosts; and (2) they indicate that the shape of the ovary, which is more or less lobed in *B. nicolli*, is entire in *B. bacciger*. However, dealing with the last point, we have found that the shape of the ovary of fellodistomids is constant in well-fixed, unflattened mature worms; but in immature worms or in poorly fixed or flattened adults the shape may be indistinct or the outline may break down. It should, therefore, be stressed that most of the material studied from the northeast Atlantic was taken from preserved fish, and Nicoll's specimens were from fishes in which 'the viscera were somewhat decomposed and the parasite badly preserved'. Hence, it would appear that the shape of the ovary is not a satisfactory differentiating character in this instance. The difference in the location of the parasite in the host does suggest a biological distinction; but, in connection with this, it would be interesting to know what the status of the stomach of *Atherina presbyter* is in relation to the physiologically stomach-less fishes mentioned by Barrington (1957). Further doubt is cast upon this distinction by the recent report of *B. bacciger* from the 'stomach' of *Boops boops* in the Adriatic Sea by Sey (1970) and of various fishes in the Mediterranean and Red Seas by Parukhin (1971, 1976). In retrospect, therefore, we do not believe that at the present time there is sufficient evidence to recognize *B. nicolli* as a distinct species.

Yamaguti (1971) included *B. nicolli* in the genus *Pseudobacciger* Nahhas & Cable, 1964. We are at a loss to comprehend this, as both published descriptions of this species clearly indicate the presence of a *cirrus-sac*!

Skrjabin & Koval (1957) suggest that *Ovotrema pontica* Pigulewsky, 1938, from the intestine of *Engraulis encrasicolus* in the Black Sea is a synonym of *B. bacciger*. This synonymy was discounted by Margolis & Ching (1965). The poor description of this species does show, however, a gross morphology similar to the baccigerines and fellodistomines. Since Pigulewsky's work both *B. bacciger* and *Pronoprymna ventricosa* have been recorded from the type-host and locality of this species, i.e. *B. bacciger* (Koval, in Skrjabin & Koval, 1957; Nikolaeva, 1963); and *P. ventricosa* (Nikolaeva, 1963). Of the two, *O. pontica* appears to be most similar to *B. bacciger*, although differing significantly in the submedian position of the genital pore and in the large size of the ventral relative to the oral sucker. When compared to the figure of *B. bacciger* from the same host and locality given by Koval, in Skrjabin & Koval (1957), however, the difference in the transverse sucker ratios, as shown in Pigulewsky' figure, is less significant. As one cannot always take inadequate descriptions at face value and because of the more recent circumstantial evidence, we accept *O. pontica* as a questionable synonym of *B. bacciger*. This species is also discussed on p. 233 and p. 259.

Genus ***PRONOPRYMNA*** Poche, 1926

Pentagramma Chulkova, 1939, *nec* Van Duzee, 1897.
Pseudopentagramma Yamaguti, 1971.

DIAGNOSTIC FEATURES. Body small, fusiform. Body-surface smooth. Cirrus-sac elongate; thin-walled; closely applied to surface of seminal vesicle. Seminal vesicle internal; bipartite. Pars prostatica short; surrounded by few gland-cells. Ejaculatory duct short. Cirrus absent as a permanent structure. Ovary median; post-testicular; irregularly trilobed. Laurer's canal opening on dorsal surface close to posterior extremity. Canalicular seminal receptacle present. Vitellarium two symmetrical compact masses composed of small follicles; masses may occasionally be dispersed; lateral or just posterior to ventral sucker. Parasitic in intestine, caeca and (?) stomach of marine teleosts.

TYPE-SPECIES. *Pronoprymna ventricosa* (Rudolphi, 1819) (by original designation).

COMMENT. The name *Pronoprymna* was introduced by Poche (1926) as a replacement name for *Pronopyge* Looss, 1899. Looss (1899) had erected and defined *Pronopyge*, quoting the type as being '*Pronopyge ocreata* (Rud.) (= *Dist. carolinae* Stossich)', and in the definition and a footnote had made it clear that he was using the description of '*Apoblema ocreatum*' by Monticelli (1891), which is clearly of a fellodistomid, in formulating his conception. Monticelli (1891) included not only *D. carolinae*, but also *D. ventricosum* Rudolphi, 1819, as a synonym of his '*Apoblema ocreatum*'. The history of *Distoma ocreatum* is rather involved and will be discussed in more detail elsewhere when discussing *Hemiurus luehei* Odhner, 1905 (Gibson & Bray, in preparation), but its early records are from the stomach and intestine of *Clupea harengus* and Rudolphi (1809), the author of the name, makes it clear that it is an appendiculate (ecsomate) form. Molin (1861) described '*Distoma ocreatum* Rudolphi' from the stomach of *Alosa alosa* at Venice, and then Monticelli (1891) presented his description of '*Apoblema ocreatum*' from the stomach of an 'alose' dissected at Naples. Odhner (1911*b* : 528 footnote) was unable to understand why Monticelli (1891) considered *D. ocreatum* and *D. ventricosum* synonymous, and, on a re-examination of Rudolphi's specimens, declared that *D. ocreatum* of Rudolphi belongs to the genus *Hemiurus* Rudolphi, 1809, and is in fact synonymous with his own species *H. luehei*.

Distoma ventricosa was originally recorded by Rudolphi (1819) from the intestine (p. 108) or stomach (p. 398) of *Alosa alosa* at Rimini. Odhner (1911*b*) also re-examined the types of this species and was convinced that they were a species of '*Pronopyge*'. The type-species of the genus *Pronopyge*, however, was originally designated as *P. ocreata* (Rud.), and, as Article 42(b) of the ICZN makes clear, the genus is 'objectively defined only by reference to its type-species' and that (Article 70) 'it is to be assumed that an author correctly identifies the nominal species that he . . . designates as the type-species of the new or of an established genus'. Poche (1926), anticipating these provisions of the ICZN, produced the new name *Pronoprymna* with the type-species *Distoma ventricosum* Rud., which, it appears, must stand as the valid name of this genus. In short, although Looss' concept of *Pronopyge* is the same as Poche's of *Pronoprymna*, the name *Pronopyge* is objectively based on Rudolphi's *D. ocreatum*, which is now known to be a *Hemiurus* and, therefore, automatically becomes a synonym of the latter genus.

An examination of the description of Molin (1861; as *Distoma ocreatum*) and Monticelli (1891 ; as *Apoblema ocreatum*: Looss' conception of *Pronopyge* is based upon this description), and a comparison with our own material, shows that we are dealing with a fellodistomid genus close to *Bacciger*. It must be more than a coincidence that Rudolphi (1819) described *Distoma ventricosum* and *D. baccigerum* next to one another. It is also apparent that the same species has been figured by van Beneden (1871), who called it *Distoma ventricosa* (p. 68) and *D. ventricosum* (p. 69), and by Stossich (1888, 1889) under the name *Distomum carolinae*. The latter two records are from *Alosa fallax* (=*finta*) off the Belgian coast and Trieste, respectively. The picture of this species that is built up from these various descriptions and figures indicates that it is the same species as was described under the name *Pentagramma symmetricum* by Chulkova (1939) and Margolis & Ching (1965) from shads in the Black Sea and as *Orientophorus caspialosae* by Kurochkin (1964) from shads in the Caspian Sea. The name *Pentagramma carolinae* (Stossich) has been used for specimens from the Black Sea region by Koval *et al.* (1973). *Pentagramma* Chulkova, 1939, is pre-occupied and has been replaced by *Pseudopentagramma* Yamaguti, 1971; but both of these names now become synonyms of *Pronoprymna*.

There appear to be two known valid species of the genus *Pronoprymna*. These are:

(1) *Pronoprymna petrowi* (Layman, 1930) n. comb. [syns. *Monorcheides* (?) *petrowi* Layman, 1930; *Orientophorus petrowi* (Layman) Mamaev, Parukhin, Baeva & Oshmarin, 1959; *Bacciger petrowi* (Layman) Zhukov, 1959; *Pentagramma petrowi* (Layman) Margolis & Ching, 1965; *Pseudopentagramma petrowi* (Layman) Yamaguti, 1971; *Orientophorus sayori* Yamaguti, 1942; *Faustula sayori* (Yamaguti) Yamaguti, 1958]; from various fishes, notably clupeids, from the North Pacific. This species is reviewed by Margolis & Ching (1965). See also p. 259).

(2) *P. ventricosa* (Rudolphi, 1891) Poche, 1926; type-species of the genus (see below).

Pronoprymna ventricosa (Rudolphi, 1819) Poche, 1926

Distoma ventricosum Rudolphi, 1819.
Apoblema ventricosum (Rudolphi) Monticelli, 1893.
Pronopyge ventricosa (Rudolphi) Odhner, 1911.

Distoma ocreatum (Rudolphi) of Molin (1859; 1861)
Apoblema ocreatum (Rudolphi) of Monticelli (1891).
Pronopyge ocreata (Rudolphi) of Looss (1899).
Distomum carolinae Stossich, 1888.
Pronopyge carolinae (Stossich) Dollfus, 1968.
Pentagramma carolinae (Stossich) Koval, Paschkevitschute, Boschko, Kovalenko & Stavrovsky, 1973.
Pentagramma symmetricum Chulkova, 1939.
Pseudopentagramma symmetricum (Chulkova) Yamaguti, 1971.
Orientophorus caspialosae Kurochkin, 1964.
Pseudopentagramma caspialosae (Kurochkin) Yamaguti, 1971.

TYPE-HOST AND LOCALITY. *Alosa alosa*, Rimini, Italy.

RECORDS

(i) Material studied

(a) From the NE Atlantic

Alosa alosa [pyloric caeca] SW Irish Shelf, Celtic Sea (Dec., 1974). Donated by A. V. Gaevskaja. BM(NH) 1978.2.22.1–2.

Alosa fallax [intestine] River Severn, England (May). Collected by C. R. Kennedy. BM(NH) 1977.10.11.1–20.

—— [?] Scarborough, North Yorkshire, England (Jan., 1978). Collected by D. Whittaker. BM(NH) 1979.2.14.20–22.

(b) From elsewhere

Alosa pontica [?] Black Sea (1968). Studied for us by A. V. Gaevskaja.

Engraulis encrasicolus [pyloric caeca] Black Sea. Collected by V. M. Nikolaeva. Material of L. Margolis.

(ii) NE Atlantic records from the literature

Alosa alosa [intestine] Belgian coast. van Beneden (1871 : 69; as *Distoma ventricosum*, but not figured or described).

—— [stomach, intestine] River Rhine at Basle, Switzerland. Zschokke (1896 : 775; as *Distomum ventricosum*, but not figured or described); Hausmann (1897 : 6, 20; as *D. ventricosum*, but not figured or described).

Alosa fallax [stomach] Belgian coast. van Beneden (1871 : 68; as *Distoma ventricosa*, figured).

Sprattus sprattus [pyloric caeca, intestine] Belgian coast. van Beneden (1871 : 67; as *Distoma ventricosum*, but not figured or described).

ASPECTS OF BIOLOGY. Nothing is known of the life-history of this worm. It appears to be a relatively common parasite of shads (*Alosa* spp.) and occurs less commonly in other fishes, notably other clupeids. It is found in the Mediterranean, Black and Azov Seas, as well as in the NE Atlantic region, and is said to occur in the South Atlantic and Red Sea (Parukhin, 1975).

PREVIOUS DESCRIPTIONS. Molin (1861 : 209; as *Distoma ocreatum*); van Beneden (1871 : plate IV, Fig. 11; as *Distoma ventricosum*); Stossich (1888 : 101; 1889 : 26; as *Distomum carolinae*); Monticelli (1891 : 508, as *Apoblema ocreatum*); Chulkova (1939 : 22; as *Pentagramma symmetricum*); Nikolaeva (1963 : 411; as *P. symmetricum*); Kurochkin (1964 : 166; as *Orientophorus caspialosae*); Margolis & Ching (1965 : 391; as *P. symmetricum*); Naidenova (1970 : 95; as *P. symmetricum*).

DESCRIPTION (Fig. 15). This description is based upon 33 whole-mounted and 7 sectioned specimens. Our observations have been supplemented by measurements and figures of specimens from both the Celtic Sea and Black Sea carried out by Dr Gaevskaja. The worms are small and have a fusiform outline (Fig. 15a & b); the dimensions are given in Table 11. As far as could be ascertained the surface of the body is smooth and does not bear spines. The subterminal, globular *oral sucker* is usually slightly smaller than the globular *ventral sucker*, which is present just inside the anterior half of the worm. There is a short prepharynx, a small, oval *pharynx* and a distinct oesophagus, which is longer than the pharynx. The caecal bifurcation occurs in the posterior forebody, and the narrow caeca reach back dorso-laterally to just beyond the testes where they end blindly.

The *excretory pore* is terminal. It leads into a vesicle which is essentially 'V'-shaped, although it has a short, narrow stem. The arms reach into the forebody to about the level of the oesophagus.

The irregularly oval to globular *testes* lie symmetrically in the anterior half of the hindbody. The vasa efferentia enter the cirrus-sac separately, but close together, The *cirrus-sac* is elongate oval, lying dorsally or dorso-laterally to the ventral sucker. Its thin wall adheres closely to the surface of a large, internal, bipartite seminal vesicle, the posterior part of which is usually the larger (Fig. 15c). The pars prostatica is short, difficult to differentiate, in fact it is almost non-existent, and there are a few external gland-cells. The ejaculatory duct is also short, and we found no evidence that a cirrus is formed, as occurs in *Bacciger*. The ejaculatory duct opens into the base of a long, narrow genital atrium (Fig. 15c); some authors have regarded this as part of the ejaculatory duct. The genital pore opens just anteriorly to the ventral sucker, and is more or less median, although it may be displaced slightly in some specimens.

The *ovary* lies in the median line just posterior to the testes. It is trilobed, although the lobes may be somewhat irregular and the lobation is often not clearly visible in poorly preserved material, or the whole ovary may be obscured by eggs. The short oviduct leaves the ovary ventrally and almost immediately receives Laurer's canal (Fig. 15d) and the common vitelline duct. The proximal region of Laurer's canal is dilated to form a canalicular seminal receptacle

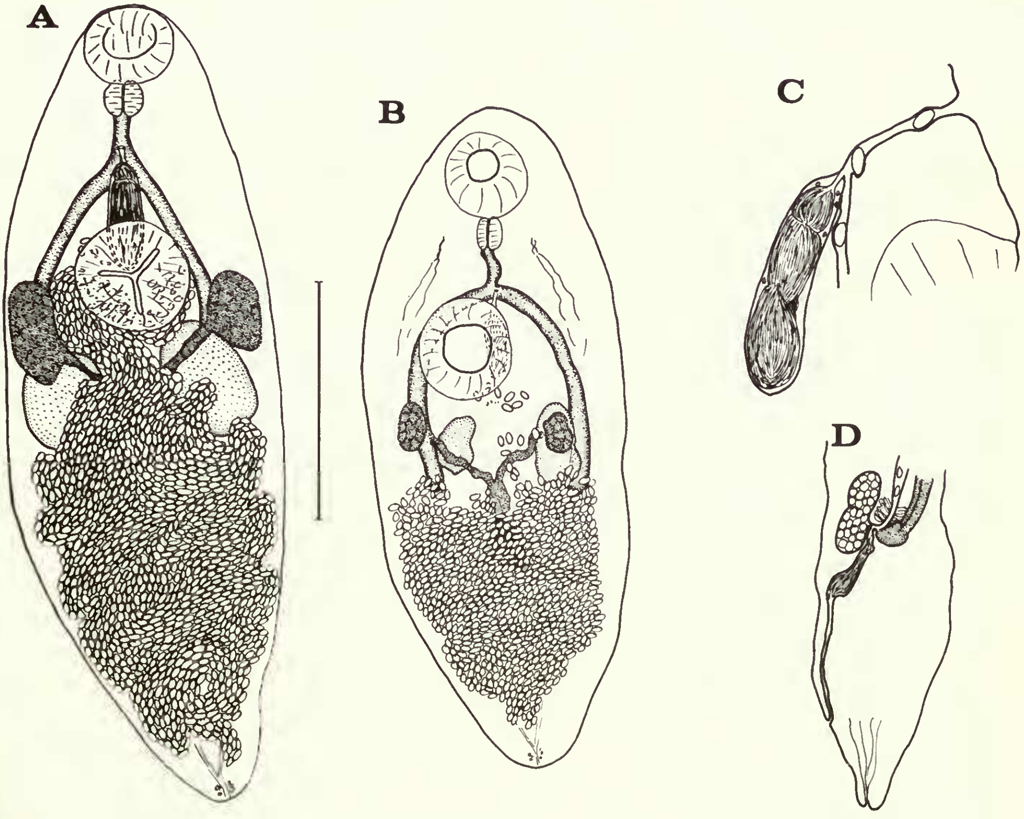

Fig. 15 *Pronoprymna ventricosa:* (a) specimen from Celtic Sea; (b) specimen from River Severn; (c) cirrus-sac; (d) diagram of female proximal genitalia and part of excretory system. Bar scale: a, b = 0·5 mm.

posterior to the ovary. It then continues posteriorly dorsal to the uterine field, before opening to the exterior on the dorsal surface close to the posterior extremity. There is no uterine seminal receptacle. The *uterus* fills most of the hindbody posterior to the testes and contains numerous operculate eggs. It is not possible to discern how the uterus coils, but the narrow distal region passes anteriorly between the testes and dorsal or dorsolateral to the ventral sucker, and unites with the ejaculatory duct at the base of the narrow genital atrium (Fig. 15c). The *vitellarium* consists of two symmetrical masses of tightly packed follicles, lying laterally or postero-laterally to the ventral sucker. Occasionally the follicles are dispersed, and more often only on one side: this effect occurs much more frequently in poorly preserved material. The thick main vitelline collecting ducts form a conspicuous 'V'-shaped structure in the middle of the body, the ducts meeting ventrally or antero-ventrally to the ovary to form a distinct vitelline reservoir of variable size (Fig. 15b & d). This reservoir is the dilated common vitelline duct.

Table 11 Dimensions of *Pronoprymna ventricosa* from the present material and from the literature

Authority	Margolis & Ching (1965)*	Gaevskaja (in litt.)	Present material	Present material	Present material
Name used	*Pentagramma symmetricum*	*Pentagramma symmetricum*	*Pronoprymna ventricosa*	*Pronoprymna ventricosa*	*Pronoprymna ventricosa*
Host	*Engraulis encrasicolus*	*Alosa pontica*	*Alosa fallax*	*Alosa alosa*	*Alosa fallax*
Locality	Black Sea	Black Sea	River Severn	Celtic Sea	Scarborough
Length (mm)	0·41–0·94	1·02–1·56	1·24–1·80	1·30–1·66	1·3–1·4
Breadth (mm)	0·17–0·32	0·34–0·36	0·40–0·74	0·51–0·67	0·43–0·48
Length : forebody ratio	1 : 0·26–0·31	(1 : 0·30)	1 : 0·24–0·30	1 : 0·25–0·27	1 : 0·25–0·27
Oral sucker (mm)	0·071–0·094; 0·09–0·10 × 0·08–0·10	0·13–0·15 × 0·15–0·16	0·13–0·20 × 0·15–0·17	0·12–0·17 × 0·14–0·18	0·11–0·15 × 0·14–0·16
Ventral sucker (mm)	0·09–0·12; 0·09–0·14 × 0·10–0·12	0·18–0·20 × 0·18–0·20	0·13–0·23 × 0·14–0·24	0·15–0·25 × 0·17–0·23	0·16–0·18 × 0·14–0·20
Sucker-ratio	1 : 1·1–1·25	(1 : 1·5)	1 : 0·9–1·3	1 : 1·02–1·20	1 : 1–1·25
Pharynx (mm)	0·039 × 0·029–0·039	0·059 × 0·051	0·055–0·060 × 0·060–0·077	0·07–0·10 × 0·06–0·07	0·05–0·08 × 0·05–0·06
Oesophagus (mm)	0·026–0·030	0·046–0·059	0·13–0·15	0·10–0·13	0·06–0·07
Cirrus-sac (mm)	–	–	–	0·14–0·23 × 0·05–0·07	0·18–0·25 × 0·05–0·07
Testes (mm)	0·071–0·15 × 0·066–0·11	0·11–0·16 × 0·081–0·12	0·18 × 0·13–0·15	0·20–0·29 × 0·17–0·21	0·17–0·22 × 0·10–0·17
Ovary (mm)	0·075–0·13; 0·13–0·12	0·16 × 0·12–0·15	–	–	–
Eggs (μm)	20–32 × 14–18	27 × 14	26–33 × 16–18	27–30 × 16–18	23–28 × 16–18

* These data include our measurements of Margolis' material.

DISCUSSION. The description above agrees closely with that of Margolis & Ching (1965) except for the interpretation of the terminal genitalia. The latter authors, when describing *Pentagramma petrowi*, considered that the ejaculatory duct is long and thin, did not apparently detect the union with the uterus at the base of the genital atrium, and thus seem to have confused the ejaculatory duct and the genital atrium. The early descriptions of Monticelli (1891) and Stossich (1889) show minor discrepancies with ours, but we have little doubt that these descriptions refer to the same species. The length of the caeca shown in the figures of these two workers is rather puzzling;

but, as in all of our whole-mounts the posterior extent of the caeca is obscured by eggs, it is likely that Monticelli and Stossich misinterpreted these structures. In some of the early descriptions, and in Looss' (1899) definition of *Pronopyge*, a small, button-shaped ecsoma is referred to; but an examination of the figures of Molin (1861) and Monticelli (1891) suggest that this is nothing more than a small protrusion surrounding the excretory pore: such a protrusion is visible in a number of the specimens from the Celtic Sea which we have examined.

Pronoprymna petrowi (Layman, 1930) is similar to *P. ventricosa*. Margolis & Ching (1965) cite three distinguishing features: sucker-ratio, position and shape of oral sucker, and position of seminal vesicle relative to ventral sucker. The combination of these three features, particularly the first two, would appear to constitute, at the present time, sufficient reason for recognizing both species although it is apparent that well-preserved specimens of the two species have not been compared in detail. Margolis & Ching suggested that there is a discontinuous distribution in the genus, with *P. ventricosa* in the Black and Azov Seas and *P. petrowi* in northern Pacific waters. The reports of *P. ventricosa* in the Mediterranean Sea and northeast Atlantic (see above), the Red Sea and South Atlantic (Parukhin, 1975), and of *P. petrowi* in the Black Sea (Naidenova, 1974) and Indian waters (Madhavi, 1975), questionable though some of these records are, decrease the likelihood that geographical isolation actually occurs.

Distoma catervarium Looss, 1896, for which Yamaguti (1971) erected the genus *Walliniella*, from the intestine of *Alosa fallax* at Cairo, is superficially similar to *P. ventricosa* and comes from one of its normal hosts. These parasites were, according to Looss (1896), poorly preserved, and it is possible, therefore, that certain of the features were misinterpreted. The supposedly post-ovarian testes, however, preclude our adding this name to the synonymy of *P. ventricosa*.

Ovotrema pontica Pigulewsky, 1938, from the intestine of *Engraulis encrasicolus* in the Black Sea, is also morphologically similar to *P. ventricosa*. It differs, however, from specimens of *P. ventricosa*, which we have examined from the same host in the Black Sea, in that it apparently possesses a dispersed, follicular vitellarium not extending into the hindbody, a submedian genital pore, and oval ovary and no distinct oesophagus. This species has been discussed on pages 233 and 254.

Subfamily **XENOPERINAE** Poche, 1926 *stat. emend.*

Proctoecinae Skrjabin & Koval, 1957.

Diagnostic features. Body small to medium-sized; cylindrical to oval, but widest at level of ventral sucker. Body-surface smooth. Oral sucker subterminal; normally smaller than ventral sucker. Ventral sucker inside anterior half of body. Prepharynx short. Pharynx large; oval to globular. Oesophagus short to apparently absent. Intestinal bifurcation in forebody. Caeca extending to or near to posterior extremity. Testes two; tandem to oblique; in mid-hindbody. Cirrus-sac elongate-oval; usually in hindbody or dorsal to ventral sucker. Seminal vesicle tubular, coiled; partly or entirely internal. Pars prostatica long, wide, filling much of cirrus-sac; with filamentous lining and many external gland-cells. Ejaculatory duct short; muscular; may form cirrus capable of great extension; muscular genital papilla present lateral to opening of male duct at base of genital atrium. Genital atrium long, narrow. Genital pore sinistrally or dextrally submedian in mid- to posterior forebody. Ovary globular to slightly lobed; pre-testicular in anterior hindbody; median to sinistral. Laurer's canal present; opening dorsally at level of gonads. Uterine seminal receptacle (?) presumed present. Canalicular seminal receptacle apparently absent. Uterus coiled mainly posterior to ovary, reaching to posterior extremity, opens into base of genital atrium immediately posterior to, at level of or immediately anterior to ventral sucker through long, muscular metraterm. Eggs numerous; small, but variable in size and shape; operculate. Vitellarium composed of elongate follicles, which may break down into small globular follicles or become inconspicuous; in two symmetrical, mainly lateral fields; in mid-hindbody or anterior to mid-hindbody. Excretory vesicle 'Y'-shaped, bifurcating in mid-hindbody; arms reaching to level of pharynx. Parasitic progenetically in marine molluscs or in intestine of marine teleosts (usually sparids or labrids).

COMMENT. When Nicoll (1915*b*) erected the genus *Xenopera* he considered it to be a hemiurid mainly because of the 'long tube-like genital sinus'; but he states that 'it cannot be considered by any means a typical member of the family'. Poche (1926) erected the family Xenoperidae in the superfamily Hemiurida [=Hemiuroidea], and this family was later placed in the suborder Hemiurata by Skrjabin & Guschanskaja (1956), but the latter authors subsequently (1958) considered it to belong to the suborder Azygiata. Dollfus (1952) drew attention to the similarities between *Xenopera* and the genus *Proctoeces* Odhner, 1911, and synonymized the two: much earlier, in 1925, in a hand-written note on his translation of Fujita (1925) held in the reprint collection of the Parasitic Worms Section, British Museum (Natural History), he stated, '*Proctoeces* Odhner 1911 = *Xenopera* Nicoll 1915'. When this parallel was drawn it was realized that the family Fellodistomidae was the most appropriate place for both *Xenopera* and *Proctoeces*. Skrjabin & Koval (1957) believed that *Gauhatiana* Gupta, 1955, *Mesolecitha* Linton, 1910, *Symmetrovesicula* Yamaguti, 1938, and *Urorchis* Ozaki, 1927, belonged to the Proctoecinae, a new subfamily of fellodistomids, but did not include *Xenopera*. However, Caballero y C. (1959), in raising the Proctoecinae to the family-rank, included the Xenoperidae as a synonym.

The name given to this subfamily depends upon the validity of *Xenopera* as a genus distinct from *Proctoeces*, as the family-group name based upon *Xenopera* is older than that based upon *Proctoeces*. *Xenopera* was erected for a new species, *X. insolita*, from the rectum of *Sparus australis* off Queensland, Australia, which Nicoll (1915*b*) described from five specimens. It is widely reckoned to be similar to *Proctoeces*, differing only in the possession of an external seminal vesicle. Some authors have, however, cast doubt upon Nicoll's observations, and both Dollfus (1952), as mentioned above, and Yamaguti (1958) have considered *Xenopera* to be a synonym of *Proctoeces*. Furthermore, *X. insolita* was considered by Freeman (1963*a*) to be a synonym of *P. subtenuis* (Linton, 1907), since, when examining many specimens of the latter species, he claimed to have found one with an external seminal vesicle. Freeman & Llewellyn (1958) described and figured *P. subtenuis*, and showed that the vasa efferentia unite at the point of entry into the cirrus-sac, and descriptions of *P. maculatus* (Looss, 1901) and its synonyms (Stunkard & Uzman, 1959; Loos-Frank, 1969; Lang & Dennis, 1976) also show that an unmodified vas deferens is either short or absent. Fujita's (1925) description of a metacercaria, *P. ostreae* from *Ostrea gigas* off Japan, shows the vasa efferentia uniting at the level of the anterior testis to form a vas deferens. If this became dilated with spermatozoa, it could form an external seminal vesicle, as in *Xenopera*. Dollfus, however, in a hand-written note on the reprint (see above) of Fujita's paper, of which he was the translator, stated, 'l'adulte de *P. ostreae* Fujita et Dollfus est peut ètre *Xenopera insolita* Nicoll (1915)'. A short vas deferens is also evident in *P. maculatus* as figured by Prevot (1965); but it is most unlike the prominent, coiled external seminal vesicle which Nicoll described in *Xenopera*.

The only other record of *Xenopera* is that of Manter & Pritchard (1962), who figured and briefly described a single specimen from an unidentified host in New Zealand and mentioned this worm '. . . only to verify the genus *Xenopera*'. Their figure shows that a distinct tubular, convoluted external seminal vesicle is present. It appears to us, therefore, that it is most likely that the possession of a long, convoluted external seminal vesicle is the normal condition in *Xenopera*, whereas, if it occurs, it is an unusual and less significant feature in *Proctoeces*. In contrast with the workers who synonymized *Xenopera* with *Proctoeces*, and with Dollfus (1965) who considered it to be a subgenus of *Proctoeces*, we prefer, until more is known about it, to accept *Xenopera* as being generically distinct, and accept the name Xenoperinae as the emended name of this subfamily.

Our concept of the subfamily Xenoperinae is based upon the genera *Xenopera* and *Proctoeces* and, in our opinion, the most important diagnostic features are the deep, narrow and extensible genital atrium, the convoluted, tubular seminal vesicle, and probably the presence of a muscular genital papilla in the base of the genital atrium beside the aperture of the male duct. As the subfamily is not well established, we have compared the data in the literature for all of the genera included in the Proctoecinae (-idae) by Skrjabin & Koval (1957) and Caballero y C. (1959), and they all lack some or all of these diagnostic features. We have, therefore, not included these genera in our concept of the subfamily.

The species of the genus *Gauhatiana* Dayal & Gupta, 1954 [originally spelt *Gauhatinae*] have been described by Gupta (1955) and Gupta & Miglani (1976). They differ from the Xenoperinae in having a spiny tegument (? lost in *G. lebedevi* Gupta & Miglani, 1974), a 'Y'-shaped excretory vesicle with short arms and a seminal receptacle. Skrjabin & Koval (1966) considered *Gauhatiana* a member of the family Walliniidae, but later (1974) omitted it from this family. Gupta & Miglani (1974, 1976) considered the genus to be a macroderoidid; but there seems no reason to disagree with Yeh & Fotedar (1958), who believed it to be a synonym of the plagiorchiid genus *Astiotrema* Looss, 1900, making *G. batrachii* Dayal & Gupta 1954, a synonym of *A. reniferum* (Looss, 1898).

The species of *Mesolecitha* Linton, 1910, have been described by Linton (1910), Manter (1947), Siddiqi & Cable (1960) and Fischthal & Thomas (1968). This genus lacks the diagnostic features of the subfamily and possesses a seminal receptacle, spines on both the cirrus and the metraterm and Linton (1910) and Fischthal & Thomas (1968) describe the tegument as finely spined. The correct systematic position of this genus is problematical.

The single species of *Symmetrovesicula* Yamaguti, 1938, has been described by Yamaguti (1938, 1953*b*). It lacks the diagnostic features of this subfamily and probably fits into the Fellodistominae, differing from the other genera of the latter group in possessing rosette-shaped clusters of vitelline follicles, an intestinal bifurcation in the hindbody and a 'V'-shaped excretory vesicle with wide arms.

The species of *Urorchis* Ozaki, 1927, have been described by Ozaki (1927), Yamaguti (1934, 1942) and Ishii (1935). Despite these four descriptions, there appears to be some confusion as to the shape of the seminal vesicle and the excretory vesicle. It appears, however, that the normal situation is a bipartite seminal vesicle and an I-shaped excretory vesicle, the latter being unknown in the Fellodistomidae. It also lacks the distinctive pars prostatica which occurs in the majority of the fellodistomids. Yamaguti (1942) considered it to be an allocreadiid genus, then later (1958) erected the allocreadiid subfamily Urorchiinae for it.

The only genus in our concept of this subfamily to occur in the north-east Atlantic region is *Proctoeces*.

Genus *PROCTOECES* Odhner, 1911

DIAGNOSTIC FEATURES. External seminal vesicle absent. Vasa efferentia unite at, or close to, base of cirrus-sac.

TYPE-SPECIES. *Proctoeces maculatus* (Looss, 1901) (by subsequent designation: Fujita, 1925 : 56).

COMMENT. Fourteen species have been assigned to this genus, seven of which we believe to be synonymous with the type-species. We consider the status of the others as follows:

(1) *Proctoeces insolitus* (Nicoll, 1915) Yamaguti, 1953; the type-species of the genus *Xenopera* Nicoll, 1915 (see above).

(2) *P. lintoni* Siddiqi & Cable, 1960; from sparid and labrid fishes in and around the Caribbean Sea. This species differs from *P. maculatus* in having a globular posterior portion in addition to the convoluted, tubular part of the seminal vesicle.

(3) *P. macrovitellus* Winter, 1954; it was pointed out by Freeman & Llewellyn (1958) that this was not a *Proctoeces*, and Winter later (1960) transferred it to the zoogonid genus *Diplangus* Linton, 1910.

(4) *P. magnorus* Manter, 1940; from *Caulolatilus anomalus* off the Pacific Coast of Mexico. This species is known only from a single specimen in which the oral sucker is larger than the slightly pedunculate ventral sucker. In addition to these features, it differs from *P. maculatus* in apparently possessing a smaller average egg-size (32–37 × 15–19 μm). Nevertheless, Freeman & Llewellyn (1958) considered it to be a synonym of *P. subtenuis* (Linton, 1907) [=*P. maculatus*]. In view of the differences listed above and until more material has been examined from the type-host and locality, we prefer to consider this species a *species inquirendum*.

(5) *P. neomagnorus* Siddiqi & Cable, 1960; this is considered a synonym of *Mesolecitha linearis* Linton, 1910, by Nahhas & Cable (1964).

(6) *P. ostreae* Fujita, 1925; described as a metacercaria which may be progenetic from the gonads of the bivalve *Crassostrea gigas* off Japan. It is said to occur as an adult in *Pagrosomus major* and *Epinephelus akaara* (Korringa, 1952), but Komiya (1965) believed that the final host was still unknown. Dollfus (see above) considered that it was possibly the metacercaria of *Xenopera insolita*.

Proctoeces maculatus (Looss, 1901) Odhner, 1911

Distomum maculatum Looss, 1901.
Distomum subtenue Linton, 1907.
Proctoeces subtenuis (Linton) Hanson, 1950.
Proctoeces erythraeus Odhner, 1911.
(?) *Proctoeces major* Yamaguti, 1934.
(?) *Cercaria tenuans* Cole, 1935.
Cercaria milfordensis Uzman, 1953.
Proctoeces progeneticus Dollfus, 1965.
Proctoeces sp. of Ichihara (1964, 1965).
Proctoeces buccini Loos-Frank, 1969.
Proctoeces scrobiculariae Loos-Frank, 1969.
Proctoeces hawaiiensis Yamaguti, 1970.

TYPE-HOST AND LOCALITY. *Labrus merula*, Trieste, Adriatic Sea.

RECORDS. All records from the NE Atlantic are from molluscs.

(i) Material studied

(a) From the NE Atlantic

Buccinum undatum [kidney] Solent, Hampshire, England. Material of F. R. Stranack.
Nucella lapillus [?] Dawlish, Devon, England (Sept., 1978). BM(NH) 1978.10.2.1.
Scrobicularia plana [kidney] Chalkwell, Essex, England. Material of J. Llewellyn.

(b) From elsewhere

Halichaeres bivittata [intestine] Bermuda (see Rees, 1970 : 205; as *Proctoeces subtenuis*). BM(NH) 1976.4.8.174.

(ii) NE Atlantic records from the literature

Buccinum undatum [kidney] Mellum Island, North Sea. Loos-Frank (1969 : 326; as *Proctoeces buccini*).
(?) —— [?] Scotland. Wootten, in White (1972 : 458; as *Proctoeces* sp.).
Scrobicularia plana [kidney] Chalkwell, Essex, England. Freeman & Llewellyn (1958 : 435; as *Proctoeces subtenuis*); Freeman (1962 : 199; 1963*a* : 113; 1963*b* : 253; as *P. subtenuis*); White (1972 : 458; as *P. subtenuis*).
—— [kidney] Whitstable, Kent, England. Freeman & Llewellyn (1958 : 435; as *Proctoeces subtenuis*).
—— [kidney] Dawlish Warren, Exe estuary, Devon, England. White (1972 : 458; as *Proctoeces subtenuis*).
—— [kidney] Estuaries of Rivers Jade and Wesef, Langwarden, West Germany. Loos-Frank (1969 : 329; as *Proctoeces scrobiculariae*).
—— [?] Burry Inlet, South Wales. James *et al.* (1977 : 13; as *Proctoeces subtenuis*).

ASPECTS OF BIOLOGY. The life-history and biology of this worm have been the object of a number of studies, and an interesting picture has emerged. It is apparent that in the warmer waters of its range, this species occurs as an adult in fishes. These fishes are normally shallow-water forms, principally labrids and sparids. This part of its range includes the shallow-waters of the Mediterranean and Black Seas, the southern North Atlantic, the eastern South Atlantic, the Caribbean

Sea, the Red Sea, New Zealand, Japanese and Hawaiian waters, the latter records indicating that it may occur widely in the shallow and warmer waters of the Pacific Ocean. There is a single report of *Proctoeces* in deep-water fishes by Kamegai (1974), who found them in *Peristedion orientale* and *Synchirops altivelis* off Japan. In the colder waters of its range in the northern hemisphere adults are found in molluscs. The degree to which the life-history is abbreviated varies. Sometimes the whole life-history apparently takes place in one host or, alternatively, adults sometimes occur in what appears to be a secondary molluscan host. Prevot (1965) and Lang & Dennis (1976), in pointing out that this so-called 'progenesis' appears to be more pronounced in temperate regions, have suggested that this may represent a mechanism to enable the species to extend into cooler waters without a dependence on its normal warm-water fish-hosts. Yet, it is apparent that several labrids and sparids are common around the British coast, and, although capable of being infested (Freeman, 1963*a*), there are no records in nature.

The daughter-sporocysts of this species have been found in the blood-vessels, blood-sinuses and digestive gland of *Mytilus* spp. Uzman (1953) described the cercariae shed by *Mytilus edulis* from the northeastern coast of the USA as *Cercaria milfordensis*, and simultaneously found ovigerous specimens of *Proctoeces* in the same host. Stunkard & Uzman (1959) found at least two sporocyst-generations, cercariae, metacercariae and ovigerous adults in this host, associating *Cercaria milfordensis* with *P. maculatus*, and postulated a telescoped or abbreviated life-history. The mother-sporocysts are globular and saccular, and each contain several daughter-sporocysts, which are simple, motile and orange. Evidently the sporocysts in the vascular system seriously reduce the efficiency of the circulatory system and destroy the gonads of the host, impair its vitality and are probably lethal. Dennis *et al.* (1974), however, found that the carbohydrate reserves and phosphatase activity of the mussel are not affected by the presence of *P. maculatus*. The cercaria is microcercous, but with a tendency to lose its tail, and possesses a 'Y'-shaped excretory vesicle. Although in some cases the entire life-history occurs in the one host, it is presumed that the mollusc is often ingested by a fish which becomes the final host. There may also be a transfer of cercariae from one mollusc to another. Lang & Dennis (1976) have summarized what is known of the seasonal incidence of *P. maculatus* in *Mytilus edulis* from the northeastern coast of the USA. Daughter-sporocysts evidently accumulate in the mussels and probably persist until the death of the host, whereas adult infestations in the kidney and pericardium of this host do not exhibit a cumulative pattern of intensity and apparently terminate annually with the death of the parasites.

Prevot (1965) discovered sporocysts of this species in *Mytilus galloprovincialis* in the Mediterranean. The second intermediate hosts he found were the polychaetes *Nereis caudata* and *Hydroides norvegica* and the molluscs *Patella coerulea* and *Acanthochites discrepens*. He was unable to find complete progenesis in *M. galloprovincialis* or *N. caudata*, many examples of which he examined, although some specimens did contain anomalous eggs. On being transferred to various fishes with a pipette, the parasites survived without maturation in *Gobius niger* and *Coris julis*, but matured in the labrid *Symphodus cinereus* [=*Crenilabrus griseus*]. Dupouy & Martinez (1973) similarly found the sporocysts in *M. galloprovincialis* and metacercariae in the polychaete *Leptonereis glauca*, and they stated that *P. maculatus* only rarely or indirectly 'castrated' this mussel.

The first intermediate host in north-eastern Atlantic waters is not known, unless *Cercaria tenuans* Cole, 1935, is a synonym of *C. milfordensis* Uzman, 1953, as tentatively suggested by Canzonier (1972). *C. tenuans* has been found in *Mytilus edulis* from Conway, North Wales and Boston, Lincolnshire, England (Coles, 1935), Padstow, Devon, England (Atkins, 1931), Ria de Arosa, northwestern coast of Spain (Canzonier, 1972) and Ria de Aveiro, Portugal (Dias & Serrano, 1972).

In our region unencysted adult specimens of *P. maculatus* occur in the kidney of the bivalve *Scrobicularia plana*. Its biology in this host has been studied by Freeman & Llewellyn (1958), Freeman (1962, 1963*a*, 1963*b*) and White (1972) from which the following data are taken. At Chalkwell in the Thames estuary every specimen of this bivalve examined was infested, and the total number of *S. plana* in the region numbered several million. The distribution, however, is restricted. It has been reported from Dawlish, Devon; but all of the specimens which we have examined from this region were uninfested. At Whitstable on the opposite bank of the Thames estuary from Chalkwell only three of many *S. plana* were found to be infested. In the severe winter of 1962–63 *S. plana* was eliminated from the part of the Thames estuary where it has been infested with *P. maculatus;* but on its return a build up of infestation was observed. Little seasonal variation occurs in the Thames estuary. Other bivalves in the Thames (e.g. *Mya* and *Macoma*) were not found to harbour *P. maculatus*. In *S. plana* an increase in the intensity of the infestation, up to a maximum of 14 per host, was found to be related to the size of the host. Parasites of varying sizes were found in the same host, so it would appear that there is no intraspecific inhibition to secondary infestations. In addition, many dead and 'petrified' worms were found in the kidneys of *S. plana*.

The environment in *S. plana* is osmotically variable, as the osmolarity of the host's body-fluids tends to follow that of the estuary. In this respect, therefore, the environment is more like that of a free-living estuarine turbellarian than a normal adult digenean. The trematode is red or pink due to the presence of a haem pigment but when the worm is in fishes this pigment declines in intensity. The haemoglobin was thought to have a respiratory function only when the oxygen tension is lowered as the valves close. Freeman (1963*b*) estimated that this oxygen store could last 25 minutes but Lee & Smith (1965) have corrected this figure to 2·5 minutes.

It has been suggested that *Proctoeces* is a recent addition to the British fauna and does not occur regularly in fish in this area, thus possibly explaining its apparent disjunctive distribution. With regard to its absence from fish-hosts, it should be pointed out, however, that there appears to be no evidence that labrid fishes which occur in the region of known foci of this parasite in *S. plana* have actually been examined. The only common labrid in the Thames estuary is *Symphodus* [=*Crenilabrus*] *melops*, which, although unlikely to feed on *S. plana*, is known to feed on *Mytilus edulis*. Attempts to infest the two labrids available in sufficient numbers at Plymouth, *Ctenolabrus rupestris* and *Symphodus melops*, have been made. Kidneys of *S. plana* from Chalkwell, where the incidence is 100%, were fed to the wrasses. Over half of these fishes were later found to be infested with *P. maculatus*; but the level of infestation decreased temporally. None were left after 6 days in *C. rupestris*; but on one occasion 5 specimens remained in *S. melops* for about 12–15 days. There were no significant morphological differences between the parasites from the invertebrate and the vertebrate hosts. The infestations in these wrasses were believed to be the result of being fed with the infested kidneys and it is possible that these parasites never survive for long in the fish-host.

'Progenetic metacercariae', or 'fully adult', *P. maculatus* have also been found in the gastropods *Buccinum undatum* (kidney) in the North Sea, *Nucella lapillus* in the English Channel (see above), *Gibbula umbilicalis* (intestine & radula) from Morocco (Dollfus, 1965, 1966), *Turbo cornutus* (kidney) from Japan (Ichihara, 1964, 1965) and *Rissoa splendida* (body-cavity) from the Black Sea (Dolgikh, 1965*b*, 1967). Loos-Frank (1969) believed that the whole life-history of this parasite could be completed in the whelk *Buccinum undatum*. Two further records, of unencysted non-ovigerous metacercariae of *Proctoeces*, may be the same species. These are those of Yamaguti (1938) from the liver of the bivalve *Brachidontes senhausi* and of Shimazu (1972) from between the epipodium and mantle of the gastropod *Haliotus discus hamai*. Both of the latter records are from Japan.

Timon-David (1934) described *Metacercaria psammechini* from the muscles of Aristotle's lantern, in the echinoderms (sea-urchins) *Psammechinus microtuberculatus* and *Sphaerechinus granularis* in the Mediterranean. He considered that it possibly belonged to *Proctoeces*, in the family Steringophoridae and pointed out that labrids commonly feed on echinoderms. In 1938, however, he stated that he was unsuccessful in his attempts at experimental 'contaminations', and his hypothetical attribution of these specimens to be Steringophoridae could not be maintained. Although certain superficial characteristics are reminiscent of *Proctoeces*, it appears that a number of features, notably the excretory system, may not conform to the fellodistomid pattern.

PREVIOUS DESCRIPTIONS. Looss (1901 : 402; as *Distomum maculatum*); Linton (1907 : 106; as *Distomum subtenue*); Odhner (1911 : 108); Vlasenko (1931 : 100); Yamaguti (1934 : 410); Manter (1947 : 321; as *Proctoeces erythraeus*; 1954 : 528; as *P. subtenue*); Hanson (1950 : 83;

figured); Koval, in Skrjabin & Koval (1957 : 394); Freeman & Llewellyn (1958 : 438; as *Proctoeces subtenuis*); Stunkard & Uzmann (1959 : 187); Manter & Pritchard (1962 : 115; figured); Freeman (1963*a* : 113; as *Proctoeces subtenuis*); Dollfus (1965 : 755; as *Proctoeces progeneticus*); Ichihara (1965 : 426; as *Proctoeces* sp.); Prevot (1965 : 178; figured); Dolgikh (1967 : 219); Naidenova (1967 : 487); Loos-Frank (1969 : 326; as *Proctoeces buccini*; 329; as *P. scrobiculariae*); Yamaguti (1970 : 39; as *Proctoeces hawaiiense*); Martinez (1974 : 39); Lang & Dennis (1976 : 66).

DESCRIPTION (Fig. 16). Six flattened whole-mounts were available for study. The subcylindrical worms taper at both ends and are widest at the level of the ventral sucker (Fig. 16a & b). The body-surface is smooth. The dimensions are included in Table 12. The subterminal *oral sucker* is smaller than the subglobular to oval *ventral sucker*, which is situated at about one-third of the body-length from the anterior end. There is a short prepharynx, a well-developed, globular *pharynx* and an oesophagus which is variable in length, normally being short or apparently absent. The intestinal bifurcation occurs in the mid-forebody, and the caeca, which are often dilate terminally, reach back to about half-way between the posterior testis and the posterior extremity of the body.

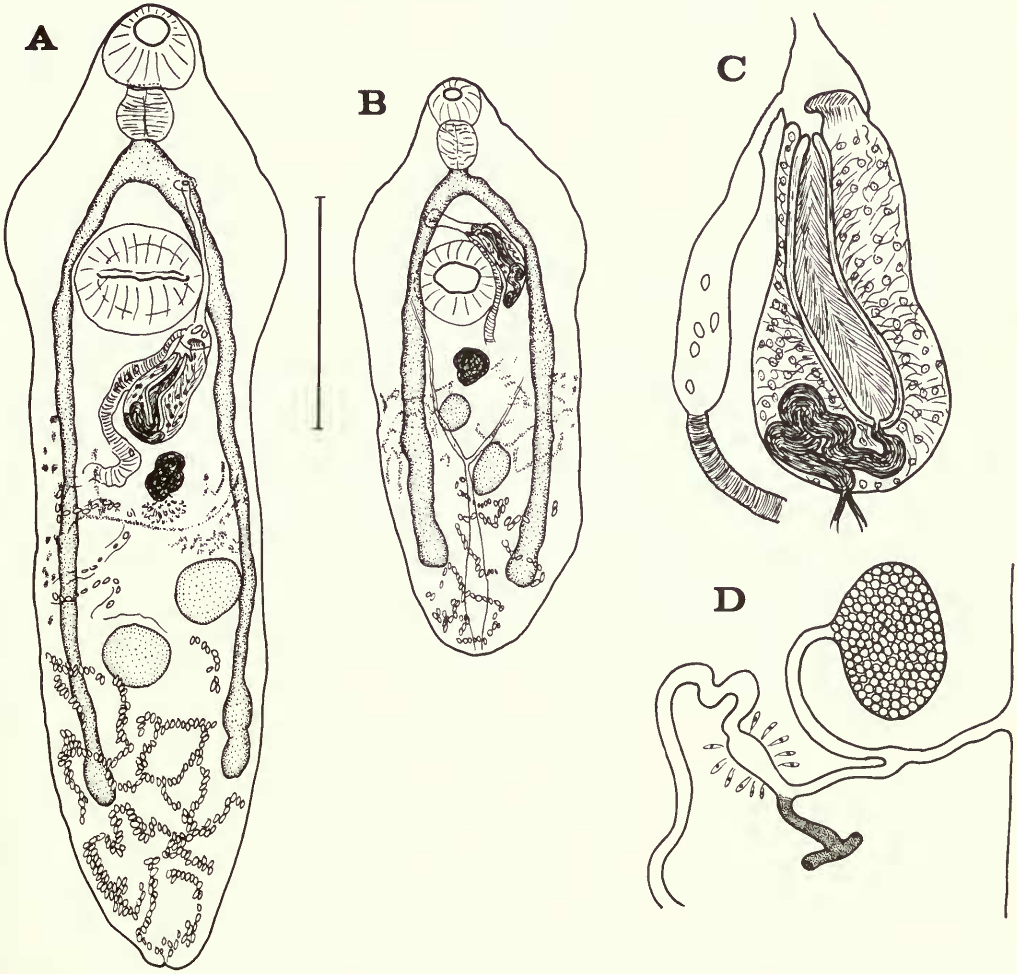

Fig. 16 *Proctoeces maculatus:* (a & b) flattened specimens – (a) ventral view of specimen from *Buccinum undatum:* (b) dorsal view of specimen from *Scrobicularia plana;* (c) cirrus–sac; (d) diagram of female proximal genitalia (modified after Freeman & Llewellyn, 1958). Bar scale: a, b = 1 mm.

Table 12 Dimensions of *Proctoeces maculatus* from the present material

Hosts	*Buccinum undatum*	*Scrobicularia plana*	*Halichaeres bivittata*	*Nucella lapillus*
Locality	Solent	Thames estuary	Bermuda	Devon
Length (mm)	2·3–4·4	2·6	1·46	1·7
Breadth (mm)	0·95–1·3	0·95–1·27	0·65	0·56
Length : forebody ratio	1 : 0·19–0·22	1 : 0·28	1 : 0·33	1 : 0·24
Oral sucker (mm)	0·27–0·36 × 0·30–0·44	0·23 × 0·23–0·24	0·20 × 0·28	0·17 × 0·18
Ventral sucker (mm)	0·40–0·54 × 0·49–0·64	0·35–0·37 × 0·42–0·43	0·33 × 0·40	0·30 × 0·38
Sucker-ratio	1 : 1·5–1·7	1 : 1·7–1·9	1 : 1·4	1 : 1·7
Pharynx (mm)	0·18–0·27 × 0·20–0·27	0·19–0·21 × 0·15–0·18	0·23 × 0·17	0·15 × 0·12
Oesophagus (mm)	0·00–0·09	0·02–0·04	0·05	0·04
Cirrus-sac (mm)	0·42–0·64 × 0·20–0·32	0·39–0·48 × 0·11–0·13	0·34–0·13	0·32–0·09
Testes (mm)	0·19–0·33 × 0·15–0·33	0·13–0·22 × 0·15–0·25	0·16–0·23 × 0·13–0·14	0·15–0·16 × 0·11–0·12
Ovary (mm)	0·19–0·23 × 0·14–0·24	0·13–0·17 × 0·14–0·18	–	0·13 × 0·13
Eggs (μm)	42–53 × 22–30	27–52 × 13–28	–	47–54 × 24–26

The terminal *excretory pore* opens into a 'Y'-shaped vesicle, which bifurcates at about the level of the testes. The arms reach anteriorly to about the level of the pharynx.

The globular or subglobular *testes* lie in tandem to obliquely in the middle of the hindbody. The vasa efferentia pass forward, uniting almost immediately before they pass through the wall of the *cirrus-sac*. The latter organ, which is elongate-oval to claviform varies in position from being entirely in the hindbody, to partly in the forebody (Fig. 16a & b), but usually lies postero-dorsal, postero-lateral, dorsal or antero-dorsal to the ventral sucker. Its actual position depends upon the degree of contraction of the genital atrium. The cirrus-sac contains the entire seminal vesicle, the pars prostatica and the ejaculatory duct (Fig. 16c). The small, tubular seminal vesicle is coiled at the proximal extremity of the cirrus-sac. The well-developed, wide pars prostatica fills much of the cirrus-sac, sometimes extending to its proximal extremity. It is almost straight to arcuate, and possesses a filamentous lining and a dense covering of gland-cells that fill much of the space remaining in the cirrus-sac. The ejaculatory duct is short, muscular and capable of being everted to form a small, conical cirrus. Beside the opening of the male duct, or the cirrus, is a prominent muscular papilla. The cirrus and associated papilla may be extruded through the genital pore in certain specimens. The genital atrium is variable in length, but is usually long (deep) and narrow (Figs 16a & b). The genital pore lies ventrally to the left of the median line at about the level of the intestinal bifurcation.

The *ovary* is globular or slightly lobed, and is usually slightly smaller than the testes. It lies anteriorly to the testes, more or less in the median line. The oviduct leaves the ovary mid-ventrally and passes posteriorly, receiving Laurer's canal, and then ventrally, receiving the common vitelline duct, before entering an inconspicuous Mehlis' gland and dilating to form a distinct oötype. Laurer's canal is short, simple and opens mid-dorsally at the level of the region between the ovary and the anterior testis (Fig. 16d). There is no seminal receptacle, and although no uterine seminal receptacle has been reported or is visible in the flattened whole-mounts which we have examined, we suggest that, in the absence of any other seminal storage mechanism, one may be present. The *uterus* is variable in size, usually extending throughout the hindbody, occasionally filling it, or sometimes consisting of only a small number of loops. It initially loops posteriorly towards the posterior extremity, whereupon it passes forward to about the level of the ovary, where it forms a distinct, muscular metraterm. The latter duct passes anteriorly more or less directly and enters the base of the genital atrium. The uterine coils, which reach extra-caecally, occur mainly posterior to the testes, lateral to the testes, and to a lesser extent between the ovary and the ventral sucker. The uterus contains numerous operculate eggs with unmodified shells. The *vitellarium* is irregularly follicular, the follicles exhibiting different degrees of development. The follicles occur in two symmetrical, lateral fields, the normal limits of distribution of which are the levels of the anterior margin of the ovary and the posterior margin of the hind testis, but they occasionally overreach these limits. Alternatively, the vitellarium may be greatly reduced or difficult to distinguish, and apparently consist of only a few scattered globular or elongate follicles (Figs 16a & b). The main transverse vitelline collecting ducts, when visible, unite postero-ventrally to the ovary and form a short common vitelline duct. The latter may swell, forming a small vitelline reservoir.

DISCUSSION. Looss (1901) originally described this species, as *Distomum maculatum*, from the labrids *Labrus merula*, *Thalassoma* [=*Crenilabrus*] *pavo* and *Symphodus cinereus* [=*Crenilabrus griseus*] in the Adriatic Sea at Trieste. Linton (1907) then described a similar worm as *Distomum subtenue* from the sparid *Calamus calamus* and the labrids *Bodianus rufus* [=*Harpe rufa*], *Halichaeres* [=*Iridio*] *bivattata* and *Lachnolaimus maximus* from off Bermuda. It was not differentiated from *D. maculatum*, but the egg-measurement given is rather smaller. Further studies, however, have shown egg-size to be a particularly unreliable criterion for this species, and no further convincing evidence has been produced to uphold the validity of *D. subtenue* as a distinct species.

In 1911 Odhner erected the genus *Proctoeces* for *D. maculatum* and a new species, *P. erythraeus*, from *Sparus* [=*Chrysophrys*] *bifasciata* and *Thalassoma* [=*Iulus*] *lunare* in the Red Sea. Subsequent studies (Hanson, 1950; Freeman & Llewellyn, 1958) have shown that *P. erythraeus*, which was originally distinguished on egg-size, sucker-size and vitelline configuration, falls well within the known morphological range of *P. maculatus*. Recent workers (Manter & Pritchard, 1962; Overstreet, 1969; Lang & Dennis, 1976) have considered both *P. subtenuis* and *P. erythraeus* as synonyms of *P. maculatus*.

Proctoeces major Yamaguti, 1934, was originally described from *Pagrosomus auratus* off Japan. It was said to differ from *P. maculatus* in having a distinctly trilobed ovary. Although in some fellodistomid groups the ovary appears to be constant, in others it varies considerably. Despite the fact that the ovary of *P. maculatus* is usually described as globular, occasional specimens of this species with a trilobed ovary have been found (Vlasenko, 1931; Freeman, 1963*b*; Dollfus, 1965). Dolgikh (1967) figured a specimen which she called '*P. major* (?)' that was found in her collection of *P. maculatus* from the gastropod *Rissoa splendida* in the Black Sea. Ichihara (1965) described *Proctoeces* sp. from the gastropod *Turbo cornutus* in Japan as having 54% of the specimens with trilobed ovaries and 46% with globular ovaries. Ichihara's specimens are herein considered to be *P. maculatus*. We tentatively include *P. major* as a synonym of this species; but we note certain morphological similarities between Yamaguti's (1934) description of *P. major* and *Xenopera insolita* Nicoll, 1915. The posterior limit of the caeca is closer to the posterior extremity than is apparent in the descriptions of *P. maculatus*, and there is a hint of an external seminal vesicle in Yamaguti's figure (1934, fig. 79).

Dollfus (1965) described *P. progeneticus* from *Gibbula umbilicalis* in Morocco. The differentiating features that he invoked are not convincing, and his specimens fit into the known variation described by Freeman & Llewellyn (1958). Dollfus' figures 2 and 3 illustrate the condition of the worm when the copulatory organ is extruded through the genital pore. The variations described by Freeman & Llewellyn also encompass the specimens described as *P. buccini* and *P. scrobiculariae* by Loos-Frank (1969). Lang & Dennis (1976) discuss the validity of *P. scrobiculariae*, giving their reasons for considering it a synonym of *P. maculatus*. In 1970 Yamaguti described *P. hawaiiense* from *Monotaxis* sp. (? *grandoculis*) off Hawaii. He differentiated it from *P. lintoni* Siddiqi & Cable, 1960, but not from *P. maculatus*, and his three specimens do not appear to be distinguishable from the latter, especially from the specimen from Hawaii figured by Manter & Pritchard (1962).

In synonymizing all of these species with *P. maculatus*, we are accepting that it must be a variable species occurring in widely dissimilar hosts. Perhaps its variability is the result of a wide host-tolerance; but both Freeman & Llewellyn (1958) and Stunkard & Uzman (1959) found a high level of variation in specimens from *Scrobicularia plana* and *Mytilus edulis*, respectively.

Subfamily **MONASCINAE** Dollfus, 1947

Haplocladinae Odhner, 1911.

Diagnostic features. Body small to medium-sized; elongate; sub-cylindrical. Body-surface smooth. Oral sucker more or less terminal; slightly larger than ventral sucker. Ventral sucker inside anterior third to quarter of body. Prepharynx absent. Pharynx elongate. Caecum single; short anterior region (? oesophagus) with tegumental lining; long posterior region with epithelial lining (? opens into excretory vesicle close to posterior extremity forming uroproct.) Testes two; tandem; usually separated by part of uterus; in posterior half of hindbody; usually sinistral. Cirrus-sac broadly oval; normally antero-sinistral or partly dorso-sinistral to ventral sucker. Seminal vesicle bipartite; internal. Pars prostatica well developed; tubular; wide; curved; with filamentous lining and many external gland-cells. Ejaculatory duct wide; muscular; diverticulate. Spermatophores occasionally seen. Genital atrium small. Genital pore sinistrally submedian; ventral in posterior half of forebody. Ovary entire to trilobed; pre-testicular; separated from anterior testis by part of uterus; sinistral in about middle of body. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Uterine coils fill much of hindbody, reaching to posterior extremity; open into base of genital atrium. Eggs numerous; small; operculate. Vitellarium follicular; in two symmetrical, lateral fields; between levels of ventral sucker and testes. Excretory vesicle 'Y'-shaped; bifurcation just posterior to ovary; arms reaching to level of pharynx or oral sucker. Parasitic in intestine of marine teleosts (predominantly Perciformes).

Comment. This subfamily contains only one genus, i.e. *Monascus* Looss, 1907, as *Haplocladus* Odhner, 1911, is clearly a synonym (see below). Travassos *et al.* (1965) raised the Monascinae to full family-status; but there are a number of features, such as the basic anatomy of the reproductive and excretory systems, which indicate that it is closely related to other fellodistomid groups. In particular, the contents of the cirrus-sac and the formation of spermatophores suggest this affinity.

Genus ***MONASCUS*** Looss, 1907

Haplocladus Odhner, 1911.

Diagnostic features. As family.

Type species. *Monascus filiformis* (Rudolphi, 1819) (by original designation).

Comment. We consider this genus to be monotypic (see below).

Monascus filiformis (Rudolphi, 1819) Looss, 1907

Distoma filiforme Rudolphi, 1819.
Haplocladus filiformis (Rudolphi) Odhner, 1911.
Haplocladus typicus Odhner, 1911.
*Monascus typicus** (Odhner) Dollfus, 1947.
Haplocladus minor Odhner, 1911.
Monascus minor (Odhner) Dollfus, 1947.
Haplocladus orientalis Srivastava, 1937.

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* *Monascus monenteron* Looss, 1907 *nomen nudum*, has been considered (e.g. Looss, 1912; Fischthal & Kuntz, 1963) a synonym of *M. typicus*.

Monascus orientalis (Srivastava) Yamaguti, 1958.
Monascus netoi Travassos, Teixeira de Freitas & Bührnheim, 1965.
Monascus chauhani Kumari, 1975.
Monascus ovilobatus Kumari, 1975†.
Monascus elongatus Karyakarte & Yadav, 1976.

TYPE-HOST AND LOCALITY. *Cepola rubescens*, Rimini, Italy.

RECORDS
(i) Material studied
(a) From the NE Atlantic
Limanda limanda [intestine] Tjarno, Sweden (Aug., 1972). Material of J. Thulin.
—— [?] Carmarthen Bay, Dyfed, Wales (Sept.–Nov., 1976). Collected by H. Al-Abdul-Jabbar. BM(NH) 1977.6.29.1–4.
Trachurus trachurus [intestine] Plymouth, Devon, England (April, 1937) (see Rees [W. J.], 1947 : 604) BM(NH) 1970.1.12.13 (May, 1972) BM(NH) 1977.6.29.5–7.
—— [intestine] Vinga, west coast of Norway (Oct., 1973). Material of J. Thulin.

(b) From elsewhere
Trachurus lathami [body-cavity] El Dique, Cumana, Sucre State, Venezuela (see Nasir & Gomez, 1977 : 70) BM(NH) 1976.3.19.8.

(ii) NE Atlantic records from the literature
(a) Mature
Limanda limanda [intestine] Kristineberg, Sweden (1898). Odhner (1911*a* : 105; as *Haplocladus minor*).
—— [intestine] Western Kattegat. Køie (1979 : 117).
Trachurus trachurus [intestine] Plymouth, Devon, England. Rees (1947 : 604; as *Haplocladus typicus*).
—— [intestine] Strait of Gibraltar. Kovaleva (1969 : 132; 1970*a* : 53; as *Haplocladus typicus*).
—— [intestine] Western Kattegat. Køie (1979: 117).

(b) Immature
Arnoglossus laterna [intestine] Western Kattegat. Køie (1979: 117).
Buglossidium luteum [intestine] Western Kattegat. Køie (1979: 117).
Crystallogobius linearis [intestine] Western Kattegat. Køie (1979: 117).
Glyptocephalus cynoglossus [intestine] Western Kattegat. Køie (1979: 117).
Pomatoschistus minutus [intestine] Western Kattegat. Køie (1979: 117).

ASPECTS OF BIOLOGY. Larval stages of *Monascus filiformis* recorded in the NE Atlantic.
Nucula nitidosa [?] Western Kattegat. Køie (1979: 114).
Nucula nucleus [digestive gland and gonads] Cawsand Bay, Plymouth Sound, Devon, England. Rees (1947 : 602; as *Haplocladus* sp.). BM(NH) 1970.1.12.14.
Nucula nucleus or *Abra* [=*Syndosmya*] *alba* [cercariae free in aquarium] Kristineberg, Sweden. Odhner (1911*a* : 105; as *Haplocladus minor*).

Rees (1947) described the cercaria, two to ten of which he found in each infested specimen of the bivalve *Nucula nucleus*. The cercariae arise from daughter-sporocysts, which, according to our observations on one of his specimens, may have a terminal birth-pore. Each cercaria is large, up to about 3 mm in length, including the long, bifurcate tail, the furcae of which are variable in size. A long caecum which does not appear to unite with the excretory vesicle and a short diverticulum were observed. Køie (1979) also described the cercaria. She found that *Limanda limanda* became infested by eating cercariae, and *Trachurus trachurus* became infested by feeding on *Crystallogobius linearis*, which eats cercariae, but in which the worm does not mature. It would

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† *Monascus chauhani* is the name given by Kumari (1975) at the head of the description, but the figure is labelled *M. ovilobatus*.

appear that sperm-transfer involves spermatophores, as these have been reported by Odhner (1911*a*) and Fischthal & Kuntz (1963).

The adult worms occur mainly in carangids, although a wide range of other fish are also infested (see below). The species has a widespread distribution, including not only the northeast Atlantic and both the Mediterranean and Black Seas, but also the Gulf of Mexico, the Atlantic coast of South America and Africa, the Pacific coast of Central America and the coastal regions of India and the Arabian peninsula.

PREVIOUS DESCRIPTIONS. Odhner (1911*a* : 104; as *Haplocladus typicus* and *H. filiformis*; 105; as *H. minor*); Vlasenko (1931 : 99; as *Haplocladus typicus*); Srivastava (1941 : 42; as *Haplocladus orientalis*); Dollfus (1947 : 319); Janiszewska (1953 : 41; as *Haplocladus typicus*); Koval, in Skrjabin & Koval (1957 : 358; as *Haplocladus typicus*); Fischthal & Kuntz (1963 : 177; as *Monascus typicus*); Nikolaeva (1963 : 413; as *Haplocladus typicus*); Travassos *et al*. (1965 : 46; 1967 : 25; as *Monascus netoi*); Lamothe-Argumedo (1969 : 179; as *Monascus typicus*); Hafeezullah & Siddiqi (1970 : 934, figure only; as *Monascus typicus*); Nahhas & Powell (1971 : 2); Fischthal & Thomas (1972*b* : 297; as *Monascus typicus*); Kumari (1975 : 248; as *Monascus chauhani* and *M. ovilobatus*); Karyakarte & Yadav (1976 : 169 as *M. elongatus*; 172 as *M. typicus*); Nasir & Gomez (1977: 70); Køie (1979: 123).

DESCRIPTION (Fig. 17). This account is based upon 15 specimens, three of which were serially sectioned. The dimensions of the worms are given in Table 13, but these preserved specimens studied were either flattened or poorly fixed. The body of these small to medium-sized worms is elongate and sub-cylindrical, possessing a smooth tegument. The body-wall contains prominent diagonal muscles. The *oral sucker* is sub-globular to slightly elongate, opens more or less terminally and may be slightly withdrawn (Fig. 17b). It is usually slightly larger than the circular *ventral sucker*, which lies in the anterior third (usually quarter) of the body. There is no prepharynx, as the oral sucker abuts directly onto an elongate and large *pharynx*, which leads into an oesophagus and a single caecum. The oesophagus is short, slightly narrower than the caecum and possesses a tegumental lining: the latter clearly distinguishes it from the caecum, which is lined by cuboidal epithelium. The caecum tends to be dorso-dextral and at the posterior end of the body, it apparently narrows to a short duct which may form a uroproct. Køie (in litt.) was unable to find a uroproct and our material is unclear in this respect. In a sectioned specimen a short caecal diverticulum was seen between the ventral sucker and the ovary, this is probably the 'reduced left caecum' of Koie (1979).

The terminal *excretory pore* leads into a narrow, 'Y'-shaped vesicle, which passes ventrally to the caecum and usually bifurcates posteriorly to the level of the ovary in fully-developed worms, although in one of our sectioned specimens the bifurcation was just anterior to the ovary. The arms reach forward into the forebody to the level of the pharynx.

The rounded *testes* lie in tandem in the hindbody. In small worms they lie close together and close to the posterior extremity; but, as the uterus grows, it appears to force them further apart and also forms a large number of coils in the post-testicular region, where the hindbody extends in order to accommodate it. This form of allometric growth has caused some confusion in the taxonomy of this genus. The testes normally lie towards the left side of the body. The vasa efferentia were not visible in our sections; but, according to Fischthal & Kuntz (1963), they unite almost immediately prior to passing through the wall of the cirrus-sac, forming a short vas deferens. The *cirrus-sac* is globular to oval, large and situated antero-sinistral to the ventral sucker, although it may be antero-dorsal in unflattened specimens. Within the cirrus-sac there is a bipartite seminal vesicle, the parts of which tend to be oval to globular, the pars prostatica and the ejaculatory duct (Fig. 17a). The seminal vesicle is small and lies in the proximal region of the cirrus-sac. The pars prostatica is tubular, wide and curved, possessing a filamentous lining and a dense external covering of gland-cells that fill much of the available space within the cirrus-sac. The ejaculatory duct is short, wide and diverticulate, and although not seen in our material, it may evert to form a conical cirrus which may protrude through the genital pore (see fig. 2 of Fischthal & Kuntz, 1963). No spermatophores were seen associated with the terminal

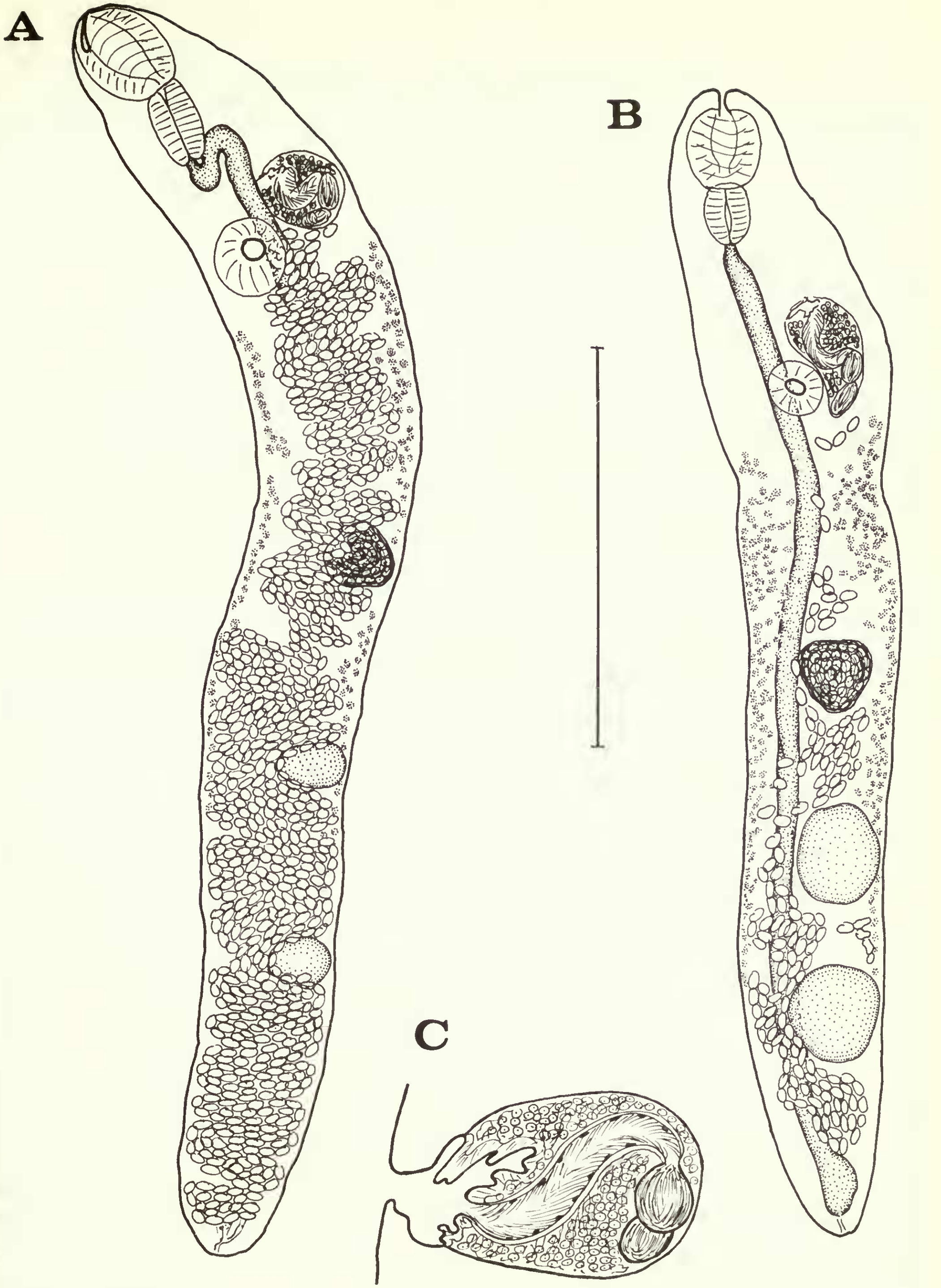

Fig. 17 *Monascus filiformis:* (a) specimen from *Trachurus trachurus:* (b) specimen from *Limanda limanda*; (c) cirrus-sac. Bar scale: a, b = 1 mm.

Table 13 Dimensions of *Monascus filiformis* from the present material and from the literature

Authority	Nasir & Gomez (1977)	Present material	Present material
Name used	*Monascus filiformis*	*Monascus filiformis*	*Monascus filiformis*
Hosts	*Trachurus lathami*	*Limanda limanda*	*Trachurus trachurus*
Locality	Venezuela	see text	see text
Length (mm)	4·3–4·9	2·8–5·3	1·3–7·6
Breadth (mm)	0·26–0·43	0·48–0·67	0·23–0·52
Length : forebody ratio	1 : 0·20	1 : 0·15–0·23	1 : 0·22–0·33
Oral sucker (mm)	0·21–0·25 × 0·13–0·19	0·21–0·35 × 0·19–0·27	0·16–0·17 × 0·13–0·22
Ventral sucker (mm)	0·13–0·23 dia.	0·14–0·25 × 0·14–0·26	0·11–0·21 × 0·11–0·21
Sucker-ratio	1 : 1	1 : 0·74–0·95	1 : 0·80–0·95
Pharynx (mm)	0·15–0·21 × 0·10–0·135	0·16–0·28 × 0·11–0·15	0·09–0·15 × 0·15–0·20
Oesophagus (mm)	–	0·045	0·02–0·14
Cirrus-sac (mm)	0·25–0·51 × 0·10–0·33	0·32 × 0·17–0·21	0·14–0·38 × 0·08–0·20
Testes (mm)	0·17–0·28 dia.	0·21–0·29 × 0·23–0·29	0·06–0·26 × 0·08–0·26
Ovary (mm)	0·17–0·21 dia.	0·18–0·20 dia.	0·07–0·23 × 0·10–0·21
Eggs (μm)	26–28 × 16–18 (our data: 34–36 × 21–25)	40–49 × 22–28	40–46 × 22–31

genitalia of our material; but their occurrence in this species has been reported (see above). The genital atrium is small and opens via the genital pore ventrally on the left side of the posterior half of the forebody.

The *ovary* varies in shape from being more or less globular to being trilobed. It lies directly anterior to the testes in small worms, but becomes separated from the anterior testis by coils of the uterus as the worm grows. In fully grown worms it is normally in about the middle of the body, but slightly towards the left side. The exact details of the remainder of the proximal region of the female reproductive system are difficult to make out in our material, and other workers do not appear to have described this region in detail. It appears, however, that the oviduct arises ventrally, passes anteriorly and is almost immediately united with Laurer's canal which opens dorsally. The oviduct then passes over the anterior surface of the ovary and receives the common vitelline duct as it passes into an indistinct Mehlis' gland situated anteriorly to the ovary. There is a small uterine seminal receptacle present. The *uterus* fills most of the hindbody, especially in the ventral field, reaching to or close to the posterior extremity, but not passing to the left of the gonads. It appears to form a simple, narrow metraterm at about the level of the ventral sucker, and this passes directly forward sinistrally or ventro-sinistrally to the cirrus-sac and enters the base of the genital atrium. The uterus contains numerous operculate eggs with smooth shells. The *vitellarium* consists of numerous small follicles in two symmetrical, lateral fields between the level of the ventral sucker and the level of the testes. The exact limits are, however, variable: the anterior limit may be just posterior to the ventral sucker, while the posterior limit varies between the anterior margin of either testis. The transverse vitelline ducts unite anteriorly to the ovary to form the common duct, which is swollen to form a small vitelline reservoir.

DISCUSSION. The genus *Monascus* was erected by Looss (1907) for *Distoma filiforme* Rudolphi, 1819, the type-species, and *M. monenteron* nom. nud. Without reference to this work Odhner (1911*a*) erected the genus *Haplocladus* for *H. typicus*, type-species, and two other species, one of which was *H. filiformis* (Rudolphi, 1819). In 1912 Looss indicated that *Monascus filiformis* and *Haplocladus filiformis* were synonymous [although erroneously referring to Rudolphi's material as *Distoma filicolle* instead of *D. filiforme*], and that *H. typicus* of Odhner was identical to his own *M. monenteron*. As Looss's comments were made in a footnote, it was not until the work of Dollfus (1947) that *Haplocladus* was generally recognized as being a synonym of *Monascus*.

We believe that all of the described species of this genus can be considered synonymous, as attempts to separate them have been unconvincing. It is evident that the continued recognition of some of the species was based, at one time, solely on the host-species. The early records of *M. filiformis* were from *Cepola rubescens*, *M. typicus* was recorded in *Trachurus trachurus* and *M. orientalis* (Srivastava, 1937) in *Synaptura orientalis*. The hosts of other species, each recorded only once , are: *M. minor* (Odhner, 1911) in *Limanda limanda; M. netoi* Travassos *et al.*, 1965, in *Oligoplites saurus*; *M. chauhani* Kumari, 1975, in *Pampus* spp. and *M. elongatus* Karyakarte & Yadav, 1976 in *Stromateus niger*. As further records of *M. filiformis*, *M. typicus* and *M. orientalis* accumulated a greater variety of hosts were recorded. The additional hosts of these species are:

M. filiformis – Carangidae – *Trachurus lathami* (Nasir & Gomez, 1977)
Decapterus punctatus (Nahhas & Powell, 1971)
M. orientalis – Nemipteridae – *Nemipterus japonicus* (Parukhin, 1973, 1976)
Serranidae – *Epinephelus ascolatus* (Parukhin, 1976)
M. typicus – Carangidae – *Trachurus mediterraneus* (Janiszewska, 1953; Nikolaeva & Kovaleva, 1966; Kovaleva, 1969, 1970*a*)
T. mediterraneus ponticus (Nikolaeva, 1963; Nikolaeva & Kovaleva, 1966; Kovaleva, 1965, 1968, 1969, 1970*a*, 1970*b*)
T. trecae (Kovaleva, 1975)
T. picturatus (Kovaleva, 1975)
Decapterus russelli (Fischthal & Kuntz, 1963; Hafeezullah & Siddiqi, 1970; Parukhin, 1976)
D. rhonchus (Fischthal & Thomas, 1968)
Selar [=*Trachurops*] *crumenophthalmus* (Fischthal & Thomas, 1968, 1972*b*; Lamothe-Argumedo, 1969; Parukhin, 1970, 1976).
Caranx hippos (Lamothe-Argumedo, 1969; Papoutsoglou, 1976).
C. armatus and *C.* sp. (Parukhin, 1976).
Chloroscombrus chrysurus (Fischthal & Thomas, 1968).
– Cepolidae – *Cepola rubescens* (Sey, 1970)
– Lethrinidae – *Lethrinus miniatus* (Parukhin, 1976).
– Stromateidae – *Pampus argenteus* (Madhavi, 1975)
Stromateus maculatus (Gaevskaja & Kovaleva, 1978)
– Clupeidae – *Sardinella aurita* (Parukhin, 1970, 1975, 1976).
– Scombridae – *Scomber colias* (Eremina, 1970)
– Balistidae – *Abalistes stellatus* (Parukhin, 1978)
– Platycephalidae – *Platycephalus macrocanthus* (Karyakarte & Yadav, 1976)
– Characidae – *Hydrocynus forskalii* (Fischthal & Kuntz, 1963).

As far as the relationships of these fishes are concerned (see Nelson, 1976), there seems to be no basis for the separation of *Monascus* on the grounds of host-group specificity. While it appears that the majority of hosts belong to the family Carangidae (*Caranx*, *Trachurus*, *Oligoplites*, *Decapterus*, *Selar*, *Chloroscombrus*), other closely related and even quite different fishes may become infested. The most closely related to the carangids are *Cepola* (Cepolidae), *Lethrinus* (Lethrinidae), *Epinephelus* (Serranidae) and *Nemipterus* (Nemipteridae), as these all belong to the suborder Percoidei, and *Stromateus* and *Pampus* (Stromateidae; not a flatfish, as referred to by Kumari, 1975) and *Scomber* (Scombridae) belong to the same order, the Perciformes. Unrelated forms belong to the Clupeiformes (*Sardinella*), Pleuronectiformes (*Limanda*, *Synaptura*), Scorpaeniformes (*Platycephalus*), Tetraodontiformes (*Abalistes*) and the essentially freshwater Cypriniformes (*Hydrocynus*).

The morphological features which have been used to distinguish the above species are mostly trivial and can be dismissed. Odhner (1911*a*) distinguishes *M. typicus* and *M. filiformis* on egg-size and colour and the position of the testes in the hindbody. As pointed out by Fischthal & Kuntz (1963) and as shown in Table 13, egg-size apparently varies considerably, and is even inconsistent amongst specimens from the same host-species. The colour of the eggs is probably a function of the degree of tanning which has taken place and, as is seen in many other fellodistomids, the degree of tanning may be correlated to the size of the eggs, which normally get smaller as the tanning becomes more intense. Skrjabin & Koval (1957) also use the position of the testes in the hindbody, in addition to the dimensions of the oral sucker, the length of the body and the posterior limit of the vitellarium, to separate *M. typicus*, *M. orientalis*, *M. minor* and *M. filiformis*. The hindbody, however is known to extend during development, becoming much longer relative to the forebody, the post-testicular region also develops allometrically and the testes separate (Dollfus, 1947; Fischthal & Thomas, 1972*b*). The size of the oral sucker and overall length are subject to great variation merely due to the growth of the worm, and the vitellarium is variable, particularly with regard to its posterior limit. Fischthal & Thomas (1968) could find no difference between *M. filiformis* and *M. typicus*, but stated that a 'final decision' on synonymy must await life-history studies. As all taxonomic criteria in this group are based upon comparative morphology, there seems to be no satisfactory basis for considering that these two species are distinct.

M. orientalis is said to differ from *M. typicus* in 'size ratio of suckers, size of various organs, extent and character of vitellaria and the topography of the gonads' (Srivastava, 1937) and the 'cephalad position of the acetabulum' (Srivastava, 1941). References to Table 13 and to Srivastava's (1941) figure suggests that these characters are more or less typical of those in *M. filiformis*. The only character which might be significant is the reported spinous nature of the tegument, but this is questionable and requires confirmation.

M. netoi is considered by Travassos *et al.* (1965) to differ from other species of *Monascus* in having a pharynx longer than the oral sucker. As they had only a single specimen there is no indication of the variation in this feature; but it is not at all dissimilar to that of *M. filiformis* as illustrated by Dollfus (1947). *M. chauhani*, according to Kumari (1975), differs from all known species of the genus in the larger size of the body, the oral sucker having a slit-like opening and the distinctly lobed ovary. However, it is not significantly larger than other records of *Monascus*, the slit-like opening of the oral sucker is probably a fixation-artifact and is known to occur in *M. filiformis* (see Fig. 17a), and the trilobation of the ovary appears to be fairly typical of some specimens of *M. filiformis*, where a range of form from virtually globular to distinctly trilobed occurs. When Madhavi (1975) found specimens of *Monascus* in *Pampus*, the same genus of host as *M. chauhani* and also off the Indian coast, he referred to them as *M. typicus*. *M. elongatus* is similar to *M. chauhani* and is here considered synonymous with *M. filiformis* for the same reasons.

Subfamily **TERGESTIINAE** Skrjabin & Koval, 1957

Diagnostic features. Body small to medium-sized; elongate; cylindrical. Most of body-surface smooth; but oral sucker normally surrounded by ring of about 13–20 muscular cephalic lobes, interrupted ventrally; 'neck'-region normally with six muscular flanges ('collarettes') on each lateral surface at about level of pharynx. Oral sucker subterminal to terminal; usually larger than ventral sucker, but may be of similar size or smaller. Globular ventral sucker in anterior half of body. Prepharynx absent. Pharynx normally well developed; elongate. Oesophagus well developed often long. Intestinal bifurcation in forebody or anterior hindbody. Caeca long, reaching close to posterior extremity; blind. Testes two; oval or irregularly oval; tandem to oblique; in posterior half of hindbody. Cirrus-sac normally bipartite; usually extending back dorsally and posteriorly to ventral sucker; posterior part elongate, normally contains seminal vesicle; anterior part globular, normally contains pars prostatica and ejaculatory duct. Seminal vesicle elongate; saccular. Pars prostatica small; vesicular; with indistinct lining. Ejaculatory duct large; muscular; complex; deeply diverticulate; may be completely everted through genital pore to form large, lobed cirrus. Genital atrium deep. Genital pore median to sinistrally submedian; ventral in posterior forebody. Ovary reniform to oval; pre-testicular; somewhat near middle of hindbody. Mehlis' gland dorsal to ovary. Laurer's canal and uterine seminal receptacle present. Uterine coils extend from ventral sucker back to posterior extremity or to level of testes; uterus opens into base of genital atrium via muscular metraterm. Eggs numerous; small; operculate. Vitellarium follicular; in two symmetrical, lateral fields in hindbody; fields may be confluent. Excretory vesicle 'Y'-shaped; bifurcation in about mid-hindbody; arms reaching to level of pharynx. Parasitic in intestine (often rectum) of marine teleosts.

COMMENT. We accept three genera in our conception of this subfamily. These are *Tergestia* Stossich, 1899, *Theledera* Linton, 1910, and *Gymnotergestia* Nahhas & Cable, 1964. In his revision of the genus *Tergestia*, Dollfus (1973) accepted *Theledera* as a subgenus of *Tergestia* on the basis of the difference in the position of the intestinal bifurcation, although earlier workers (Manter, 1940; Siddiqi & Cable, 1960) had synonymized the two genera. From Dollfus' work, it appears, however, that the material of Siddiqi & Cable and that of Manter, described later (1947), are specimens of *Tergestia* and not *Theledera*. We accept *Theledera* as a valid genus because of the distinct differences in the position of the intestinal bifurcation, it being in the forebody in *Theledera* and either postero-dorsal to the ventral sucker or clearly in the hindbody in *Tergestia*. We also note that in *Theledera* there is a tendency for the uterus not to reach beyond the testes, whereas in *Tergestia*, in mature specimens, it usually reaches posteriorly to the testes: there are, however, several exceptions to this. We note that there appear to be certain differences in the shape of the cirrus-sac in the species described in the literature. We consider, however, that the normal situation is that the cirrus-sac is bipartite and that the seminal vesicle occupies much of the posterior part. Examples of such variations on this pattern include *Tergestia kuhliae*, described by Yamaguti (1970), where the pars prostatica apparently occurs in the posterior part of the cirrus-sac and *Gymnotergestia chaetodipteri*, described by Nahhas & Cable (1964), where the cirrus-sac does not appear to be bipartite, although one of the figures does suggest a slight constriction. In some descriptions the exact shape of the cirrus-sac was not clearly indicated. *Gymnotergestia* differs from both *Tergestia* and *Theledera* in lacking the elaborate muscular ornamentation on the forebody and around the oral sucker: this is replaced by superficial tegumental annulations in the anterior forebody. It also differs from *Tergestia* in having the intestinal bifurcation in the forebody and apparently from both genera, as mentioned above, in having a less distinctly bipartite cirrus-sac. Only *Tergestia* occurs in the northeast Atlantic region.

While *Gymnotergestia* is monotypic, *Theledera*, of which *Cithara* MacCallum, 1917, and *Tergestina* Nagaty & Abdel Aal, 1964, are clearly synonyms, appears to contain several species. These are:

(1) *Theledera abusherai* (Nagaty & Abdel Aal, 1964) n. comb., a poorly described species from *Platax* sp. in the Red Sea. It is similar to *T. pectinata*.
(2) *Theledera acanthocephala* (Stossich, 1887) n. comb., a poorly known species found in various teleosts in the Mediterranean and Red Seas.
(3) *Theledera kuhliae* (Yamaguti, 1970) n. comb., from *Kuhlia sanvicensis* off Hawaii.
(4) *Theledera plataxi* (Nagaty & Abdel Aal, 1964) n. comb., a poorly described species from *Platax* sp. in the Red Sea. It is similar to *T. pectinata*.
(5) *Theledera pectinata* (Linton, 1905) Linton, 1910; the type-species of the genus. It is known to occur in *Chloroscombrus* and *Auxis* off the eastern coast of the USA. Most of the records of this species are in fact *Tergestia manteri* (see Dollfus, 1973).
(6) *Theledera priacanthi* (MacCallum, 1917) n. comb., from *Priacanthus cruentatus* off New York, USA.
(7) *Theledera skrjabini* (Koval & Zarichkova, 1964) n. comb., from *Symphodus* [=*Crenilabrus*] *tinca* in the Black Sea. Specimens recorded from the same host in the Mediterranean by Sey (1968) as *Tergestia laticollis* may be the same species. *T. skrjabini* appears to be similar to *T. pectinata* and somewhat similar to *T. acanthocephala*.
(8) *Theledera karachiense* Bilqees, 1978, from *Stromateus sinensis* off Pakistan.

It seems likely that many of the species of this genus are synonymous.

Genus *TERGESTIA* Stossich, 1899

DIAGNOSTIC FEATURES. Cephalic lobes around oral sucker present. Six muscular flanges ('collarettes') present on each lateral surface at level of pharynx. Intestinal bifurcation in hindbody or postero-dorsal to ventral sucker. Cirrus-sac normally distinctly bipartite. Tendency for uterus to extend into post-testicular field in mature worms.

TYPE-SPECIES. *Tergestia laticollis* (Rudolphi, 1819) (type by subsequent designation: Yamaguti, 1953*a* : 26).

COMMENT. The species we include in this genus are:
(1) *Tergestia acuta* Manter, 1947; from *Caranx* spp. off Florida, Jamaica and Belize.
(2) *Tergestia agnostomi* Manter, 1954; recorded as an immature form from both the teleost *Aldrichetta forsteri* (see Angel, 1960) and the ctenophore *Pleurobrachia pileus* (see Boyle, 1966) off New Zealand. The gravid worm has been described by Jones (1978) from *A. forsteri*.
(3) *Tergestia clonacantha* Manter, 1963; from *Hemirhamphus* spp. off Fiji, New Caledonia and India.
(4) *Tergestia haswelli* Dollfus, 1927; known only as a cercaria from *Mytilus latus*, New Zealand. We are tentatively retaining this species in *Tergestia*.
(5) *Tergestia manteri* Dollfus, 1973; from various teleosts off the eastern coast of the USA and Puerto Rico. This is a new name for *Tergestia pectinata* of Manter (1947), Hopkins (1940) and Siddiqi & Cable (1960).
(6) *Tergestia magna* Korotaeva, 1972; from *Plagiogeneion macrolepis* and *Emmelichthys nitidus* in the Great Australian Bight.
(7) *Tergestia mauritanica* Dollfus, 1973; from *Pomatomus saltator* (=*saltatrix*) off Mauritania.
(8) *Tergestia pauca* Teixeira de Freitas & Kohn, 1965; from *Scombroides* sp. off Brazil.
(9) *Tergestia laticollis* (Rudolphi, 1819) Stossich, 1899; type-species of the genus (see below). *Tergestia acanthogobii* Yamaguti, 1938, from *Acanthogobius flavimanus* off Japan is herein considered to be a synonym of this species.

As with *Theledera*, it is likely that many of the above species are synonyms.

Tergestia laticollis (Rudolphi, 1819) Stossich, 1899

Distoma laticolle Rudolphi, 1819.
Echinostoma laticolle (Rudolphi) Parona, 1899.
Distoma polonii Molin of Olsson (1868).
Tergestia acanthogobii Yamaguti, 1938.
Tergestia acanthocephala (Stossich) of Baylis (1939).

TYPE-HOST AND LOCALITY. *Trachurus trachurus*, Rimini, Italy.

RECORDS
(i) Material studied
(a) From NE Atlantic region

Scomber scombrus [stomach] Plymouth, Devon, England. Collected by P. G. Corbin (see Baylis, 1939 : 482; as *Tergestia acanthocephala;* and Prudhoe & Baylis, 1957 : 83). BM(NH) 1937.8.6.141.

Trachurus trachurus [intestine] Firth of Forth, Scotland (Aug., 1963). Collected by K. MacKenzie. BM(NH) 1977.6.17.1.

—— [intestine] Bay of Biscay (46°N, 03°W; depth 132–136 m; Jan., 1971). BM(NH) 1977.6.17.2.

—— [intestine] Plymouth, Devon, England (May, 1972). BM(NH) 1977.6.17.3–10.

—— [rectum & intestine] Off NW Scotland (58°N, 08°W; depth 116–120 m; July, 1976; and 59°N, 05°W; depth 92–120 m; July, 1976). BM(NH) 1977.6.17.11–14.

—— [intestine] Vinga, west coast of Norway (Oct., 1973). Material of J. Thulin.

(b) From elsewhere
Nil

(ii) NE Atlantic records from the literature

Scomber scombrus [stomach] Plymouth, Devon, England. Baylis (1939 : 482; as *Tergestia acanthocephala*; material redetermined by Prudhoe & Baylis, 1957 : 83).

Trachurus trachurus [intestine] Bergen, Norway. Olsson (1968 : 29; as *Distoma polonii*; material redetermined by Odhner, 1911*a*, : 112).
—— [?] Wimereux, Pas de Calais, France. Monticelli (1890 : 422; as *Distomum laticolle*).
—— [intestine] Aberdeen, Scotland. Nicoll (1913 : 192).
—— [intestine] Plymouth, Devon, England. Nicoll (1914 : 483).
—— [intestine] Strait of Gibraltar. Kovaleva (1969 : 132; 1970*a* : 53).

ASPECTS OF BIOLOGY. There is one record which is probably of a cercaria of the genus *Tergestia* in the northeast Atlantic region. This is of a free-floating form off the coast of Portugal which was referred to by Kent (1871 : 270) as a larva of '*Echinorhynchus*'. It was named *Cercaria kenti* by Dollfus (1927 : 112). The complete life-history of members of this genus is, however, not known, although sporocysts have been recorded in the mussel *Mytilus* (Haswell, 1902; Angel, 1960) in New Zealand and, in addition to the record above, cercariae have been found free in plankton by Dubois *et al.* (1952), as *Cercaria mathiasi*, in the Mediterranean Sea. The cercaria bears the characteristic ring of muscular lobes around the oral sucker and the row of collarettes in the 'neck'-region; but, according to Angel (1960), 'the unique feature of the cercaria is the tail, in which, between the main stem and the body of the cercaria, is an inflated region bearing a prominent crest dorsally'. Angel also notes that 'Haswell's observations regarding the presence of "cystogenic" cells throughout the body of *Cercaria haswelli* suggests that there is a true cyst stage'. The only record of a metacercaria, however, is of *T. agnostomi* unencysted in the gastrovascular system of the ctenophore *Pleurobrachia pileus* (see Boyle, 1966) also from off New Zealand.

Tergestia laticollis is found mainly in carangid fishes and, in our area, almost entirely in *Trachurus trachurus*. It is widely distributed in the northern hemisphere, having been recorded in the Atlantic as far south as Morocco, the Caribbean, Mediterranean and Black Seas, in the Pacific Ocean as far south as the South China Sea and Hawaii and in the Indian Ocean; but it has not been found in arctic waters. The latter phenomenon is probably because its fish-hosts tend to be restricted to temperate and tropical waters.

PREVIOUS DESCRIPTIONS. Olsson (1868 : 29; as *Distoma polonii*); Monticelli (1890 : 422; as *Distomum laticolle*); Odhner (1911*a* : 111); Nicoll (1913 : 192); Vlasenko (1931 : 101); Yamaguti (1934 : 409; 1938 : 96, 97, as *Tergestia acanthogobii*; 1940 : 88; 1951 : 271; 1970 : 39); Manter (1940 : 408; 1947 : 322); Skrjabin & Koval (1957 : 426); Siddiqi & Cable (1960 : 284, figure only); Mazza (1963 : 441); Nikolaeva (1963 : 414); Sey (1968 : 8); Dollfus (1973 : 284).

DESCRIPTION (Figs 18 & 19). The material studied comprised 19 specimens of which 3 were serially sectioned. The worms are elongate and cylindrical in cross-section. Their dimensions are included in Table 14. The widest point of the body may occur at the level of the ventral sucker (Fig. 18a), or further back in the hindbody. The body surface is smooth; but the oral sucker is surrounded by a ventrally interrupted 'halo' of 13 muscular projections (lobes). Each lobe is a roughly conical, muscular body which is overlain with tegument (Fig. 18d). The musculature is similar to that of the oral sucker; but, although the bases of the 13 lobes are fused and lie close to this sucker, they are not continuous with it. A small tegumental papilla is sometimes visible ventral to the ring of lobes. In addition, 6 flanges or 'collarettes' of histologically similar construction lie along the body-surface on either side of the pharynx and/or the oral sucker (Fig. 18e). The body-wall of this worm contains prominent diagonal muscles. The *oral sucker* is slightly longitudinally elongate with a slit-like almost terminal or subterminal opening. The *ventral sucker* is more or less globular and possesses a narrow opening, which may face forwards, backwards or laterally. It is wider than the oral sucker in the ratio of about 1 : 1·1–1·6 (1·1–1·6 in contracted specimens; 1·3–1·6 in well-fixed specimens; 1·75 in a flattened specimen), and occurs well inside the anterior half of the body. There is no prepharynx, the oral sucker leading directly into a large, elongate *pharynx*. This in turn leads into a long, narrow oesophagus, which reaches back into the anterior hindbody or postero-dorsally to the ventral sucker before bifurcating. The two narrow caeca extend back almost to the posterior extremity of the body before terminating blindly.

The terminal *excretory pore* leads into a 'Y'-shaped vesicle, which was traced as far forward as

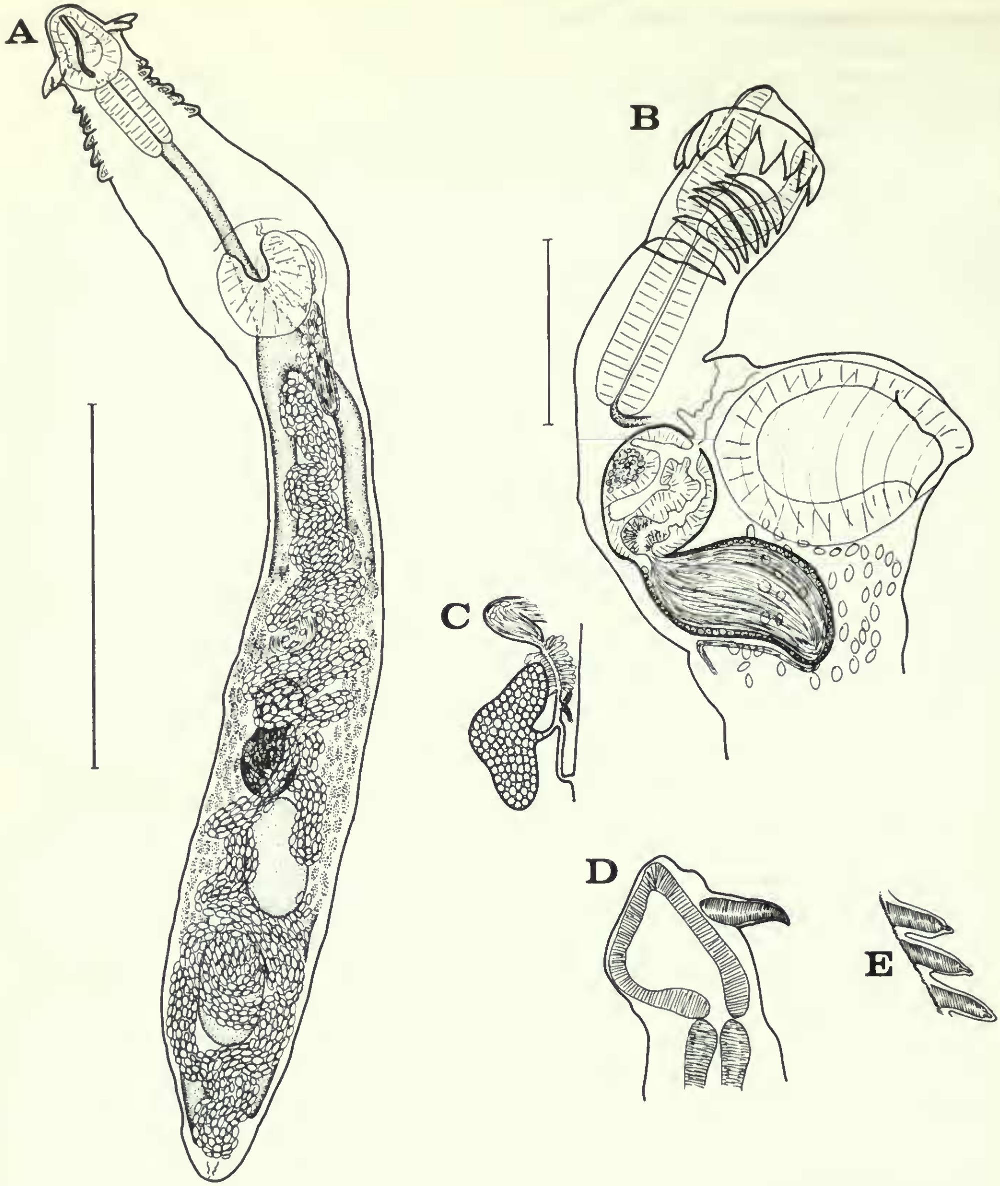

Fig. 18 *Tergestia laticollis:* (a) specimen from *Trachurus trachurus*; (b) forebody showing cirrus-sac; (c) diagram of female proximal genitalia; (d) section of anterior part of worm showing papilla-like protuberance; (e) section of 'collarettes'. Bar scale: a = 1 mm; b = 0·2 mm.

the posterior testis in a sectioned mature specimen before being obliterated by eggs. Two narrow, muscular arms were traced from the anterior hindbody as far forwards in the forebody as the level of the pharynx. Indications from the literature are that the bifurcation occurs somewhere near the middle of the hindbody.

The two *testes* are irregularly oval to elongate oval and lie almost in tandem to obliquely in the posterior half of the hindbody. The union of the vasa efferentia was not traced, but a single muscular tube has been traced from the proximal end of the withdrawn cirrus-sac, along the dorsal surface, and then passing posteriorly. The *cirrus-sac* is clearly divided into two distinct parts (Fig. 18b). The proximal part is elongate and normally reaches well into the hindbody. It contains an elongate, saccular seminal vesicle, which is surrounded by a layer of what are probably prostatic gland-cells. The distal part of the cirrus-sac is globular, and contains the pars prostatica and ejaculatory duct. The pars prostatica is small, vesicular and possesses an indistinct lining. There are also gland-cells in the distal region of the cirrus-sac (Fig. 18b), and these may also be prostatic. The ejaculatory duct is well developed, large, wide and deeply diverticulate (Fig. 18b). During copulation it appears that the whole of the ejaculatory duct is extruded through the genital pore to form a large, complex and deeply lobed cirrus. This condition is also visible in some fixed specimens (Fig. 19). When this extrusion occurs the proximal part of the cirrus-sac is pulled anteriorly to lie antero-dorsally to the ventral sucker. At rest, however, the ejaculatory duct opens into the base of a deep genital atrium, which itself opens via the genital pore ventrally and sinistrally submedian in the posterior forebody.

Table 14 Dimensions of *Tergestia laticollis* from the present material and from the literature

Authority	Odhner (1911*a*)	Yamaguti (1951)	Present material	Present material
Name used	*Tergestia laticollis*	*Tergestia laticollis*	*Tergestia laticollis*	*Tergestia laticollis*
Hosts	*Trachurus trachurus*	*Caranx equula*	*Scomber scombrus*	*Trachurus trachurus*
Locality	Palermo, Trieste	Japan	Plymouth	see text
Length (mm)	up to 4 mature at 1·5	1·6–3·5	0·97	0·80–4·6
Breadth (mm)	0·2–0·33	0·3–0·6	0·46	0·26–0·76
Length : forebody ratio	(1 : 0·26)	–	1 : 0·33	1 : 0·20–0·31
Oral sucker (mm)	0·16–0·18	0·16–0·28 × 0·13–0·23	0·17 dia.	0·16–0·21 × 0·14–0·24
Ventral sucker (mm)	0·17–0·20 × 0·20–0·23	0·30–0·46 × 0·27–0·50	0·27 × 0·22	0·18–0·37 × 0·20–0·41
Sucker ratio	(1 : 1·06–1·1)	(1 : 1·65–1·88)	1 : 1·6	1 : 1·1–1·75
Pharynx (mm)	0·08–0·10 × 0·17–0·25	0·17–0·23 × 0·08–0·13	0·10 × 0·15	0·18–0·26 × 0·07–0·12
Oesophagus (mm)	–	0·6–1·1	0·22	0·61–0·90
Cirrus-sac (mm)	–	0·26–0·53 × 0·04–0·08	–	0·30–0·74 × 0·17–0·28
Testes (mm)	–	0·16–0·40 × 0·075–0·25	–	0·10–0·25 × 0·095–0·39
Ovary (mm)	–	0·17–0·33 × 0·10–0·15	–	0·13–0·23 × 0·12–0·35
Eggs (μm)	21–23 × 15	24 × 15–18 (alive) 21–30 × 16–18 (fixed)	23–24 × 13–15	24–28 × 14–17

The elongate-oval or roughly reniform *ovary* lies anteriorly to the testes in about the middle of the hindbody. The oviduct arises from the concave dorsal surface and passes towards Mehlis' gland which lies dorso-laterally to the ovary. Prior to entering Mehlis' gland it receives firstly Laurer's canal and then the common vitelline duct. Laurer's canal is short and opens dorsally at about the level of the posterior margin of the ovary (Fig. 18c). The *uterus* passes forward from Mehlis' gland, initially forming a tightly convoluted uterine seminal receptacle. Before reaching the ventral sucker it loops posteriorly and passes to the posterior extremity, whereupon it loops forward again, thus filling much of the available space in the hindbody. In larger mature specimens the uterus reaches into the region posterior to the testes. At about the level of the ventral sucker it forms a narrow, muscular metraterm, which passes forward dorsally or dorso-laterally

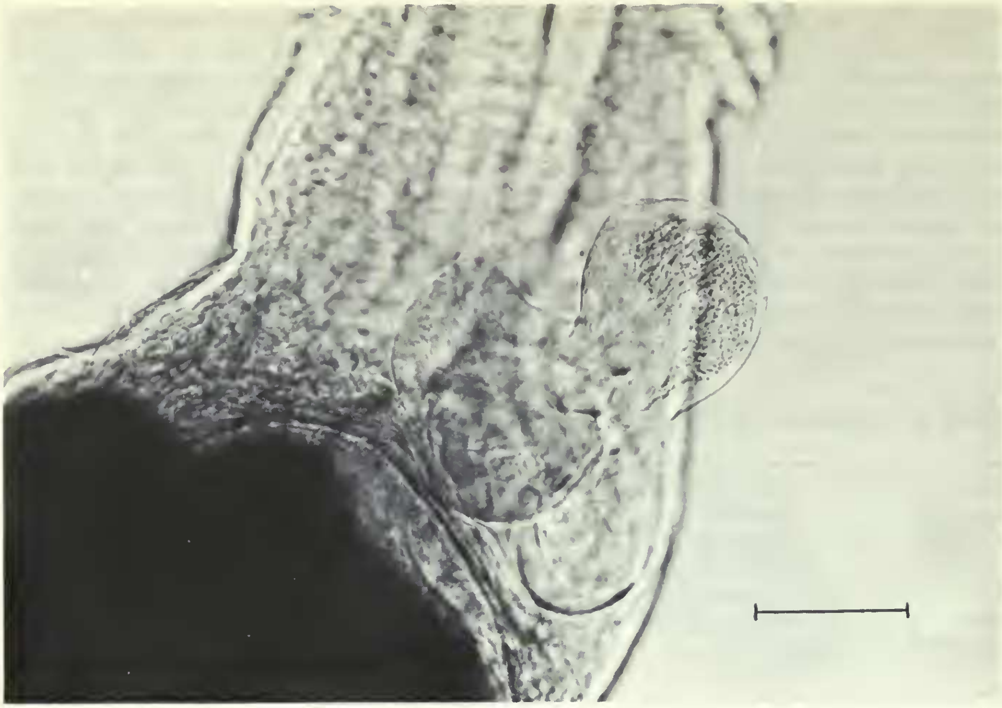

Fig. 19 Forebody of *Tergestia laticollis* with everted lobate cirrus. Bar scale: = 0·1 mm.

to this sucker and enters the base of the genital atrium. The uterus contains numerous operculate eggs. The *vitellarium* consists of a system of irregular, elongate follicles in two symmetrical, lateral fields. The extent of these fields is variable. Anteriorly the fields may only reach as far as midway between the ovary and the ventral sucker; but, in smaller and contracted specimens, the vitellarium may extend right up to the ventral sucker. The posterior limit of the fields varies between the posterior margins of either of the testes. There are also follicles in the mid-dorsal region of the body at the anterior of the vitellarium; thus in this region the fields are usually confluent. The main lateral vitelline ducts unite at about the level of the anterior margin of the ovary to form a short, simple common duct.

DISCUSSION. *Tergestia* can conveniently be split into three groups on the basis of sucker-ratios, although the status of these groups is far from clear. In two species, *T. agnostomi* and *T. haswelli*, the ventral sucker is smaller than the oral sucker; the latter is known only as an immature form, and it is possible that allometric growth occurs. Another group of species, which include *T. manteri*, *T. mauritanica*, *T. pauca* and probably *T. laticollis* of Yamaguti (1938, 1940, 1970), have a ventral sucker which is about twice the size of the oral sucker. The remainder of the species have sucker-ratios between 1 : 1 and 1 : 1·7. Our material indicates that this is about the normal variation of *T. laticollis* in the northeast Atlantic region. *T. laticollis* differs from the other species in this group thus:

(1) *T. acuta* Manter, 1947; this species has a sucker-ratio of 1 : 1·7, which is at the upper limit of the variation in our material of *T. laticollis*; the hindbody is small and pointed; and the eggs (17–19 × 9–10 μm) are smaller.

(2) *T. clonacantha* Manter, 1963; the proportion of the uterus posterior to the testes is greater in this species; the eggs (15–17 × 9–12 μm) are smaller; and in some specimens the vitelline follicles reach close to the posterior extremity. Hafeezullah & Siddiqi (1970) figure this species from India, but Dollfus (1973) considered that these are not *T. clonacantha*, as 'les lobes céphalique sont très différents et les protubérances collaires ont un emplacement un peu différent'. It appears, however, that Manter's description of the cephalic lobes as being

11 in number, with the two inner (ventral) lobes divided, is nothing more than a description of the normal condition of this genus, where, in fact, all of the 13 lobes are joined at their bases. In addition, the position of the collarettes in this genus is variable, as can be seen in our figures of *T. laticollis*: in two specimens fixed in the same way, one has the 'collarettes' reaching back to the level of the base of the pharynx (Fig. 18a) and the other has most of the 'collarettes' lateral to the oral sucker (Fig. 18b).

(3) *T. magna* Korotaeva, 1972; this species is similar to *T. laticollis*; but the eggs are smaller (quoted as 11–18 × 11–15 µm; 12 × 12 µm in life); and the edges of the 'collarettes' are crenulate.

Yamaguti (1938) provisionally considered his *T. acanthogobii* as distinct from *T. laticollis* 'because of its entirely different habitat'. Morphologically it is indistinguishable from *T. laticollis*, and we, therefore, consider it to be a synonym. The position of the three lots of *T. laticollis* described by Yamaguti (1938, 1940, 1951) with apparent sucker-ratios of almost 1 : 2, is problematical; but, as these worms are not illustrated and as we have calculated these ratios from the range of sucker-sizes given, we are not inclined to place too much emphasis on this difference. It may well be that the sucker-ratio is an unreliable feature as far as this genus is concerned, especially if the worms are flattened, and that many of the species are conspecific with *T. laticollis*.

With reference to the previous descriptions, Mazza (1963) gave the egg-measurements of *T. laticollis* as being 82–86 × 32–34 µm and Sey (1968) gave the oral sucker-size as being 5·5 mm; both of these must be considered as either typographical or technical errors. Sey (1968) also gave a measurement of 0·046–0·080 mm for the oesophagus, which suggests that it is short and, therefore, bifurcates in the forebody. This being the case, Sey could well have been dealing with specimens of *Theledera skrjabini* (see p. 275), which is found in similar hosts in the Black Sea.

Host–parasite list

Order Clupeiformes

Alepocephalus bairdii Goode & Bean : *Olssonium turneri* gen. et sp. nov.
Steringophorus pritchardae (Campbell).
Alosa alosa (Linnaeus) : *Pronoprymna ventricosa* (Rudolphi).
Alosa fallax (Lacepéde) : *Pronoprymna ventricosa* (Rudolphi).
Sprattus sprattus (Linnaeus) : *Pronoprymna ventricosa* (Rudolphi).
Xenodermichthys socialis Vaillant : *Steringophorus blackeri* Bray.

Order Notacanthiformes

Polyacanthonotus rissoanus (Filippi & Verany) : *Prudhoeus nicholsi* gen. et sp. nov.

Order Gadiformes

Ciliata mustela (Linnaeus) : *Steringotrema divergens* (Rudolphi).
(?) *Gadus morhua* Linnaeus : *Steringophorus furciger* (Olsson).
Onogadus argentatus (Reinhardt) : *Steringophorus thulini* sp. nov.
Rhinonemus cimbrius (Linnaeus) : *Steringophorus thulini* sp. nov.
Trachyrincus trachyrincus (Risso) : *Steringophorus thulini* sp. nov.

Order Zeiformes

Capros aper (Linnaeus) : *Steringotrema divergens* (Rudolphi).

Order Perciformes

Anarhichas denticulatus Krøyer : *Steringophorus furciger* (Olsson).
Anarhichas lupus Linnaeus : *Fellodistomum fellis* (Olsson).
Steringophorus agnotus (Nicoll).
Anarhichas minor Olafsen : *Fellodistomum fellis* (Olsson).
Steringophorus agnotus (Nicoll).

Blennius ocellaris Linnaeus : *Steringotrema divergens* (Rudolphi).
Crystallogobius linearis (von Düben) : *Monascus filiformis* (Rudolphi).
Lycenchelys sarsi Collett : *Steringophorus furciger* (Olsson).
Lycodes esmarki Collett : *Steringophorus furciger* (Olsson).
Lycodes pallidus Collet : *Steringophorus furciger* (Olsson).
Lycodes vahli Reinhardt : *Steringophorus furciger* (Olsson).
Steringotrema ovacutum (Lebour).
Lycodes sp. : *Steringophorus furciger* (Olsson).
Pagellus bogaraveo (Brünnich) : *Steringotrema pagelli* (van Beneden).
Pomatoschistus minutus (Pallas) : *Monascus filiformis* (Rudolphi).
Scomber scombrus Linnaeus : *Tergestia laticollis* (Rudolphi).
Spondyliosoma cantharus (Linnaeus) : *Steringotrema pagelli* (van Beneden).
Trachurus trachurus (Linnaeus) : *Monascus filiformis* (Rudolphi).
Tergestia laticollis (Rudolphi).

Order Atheriniformes
Atherina presbyter Cuvier : *Bacciger bacciger* (Rudolphi).

Order Scorpaeniformes
Gymnacanthus tricuspis (Reinhardt) : *Steringophorus furciger* (Olsson).

Order Pleuronectiformes
Arnoglossus laterna (Walbaum) : *Monascus filiformis* (Rudolphi).
Buglossidium luteum (Risso) : *Monascus filiformis* (Rudolphi).
Glyptocephalus cynoglossus (Linnaeus) : *Monascus filiformis* (Rudolphi).
Steringophorus furciger (Olsson).
Hippoglossoides platessoides (Fabricius) : *Steringophorus furciger* (Olsson).
Steringotrema ovacutum (Lebour)
Limanda limanda (Linnaeus) : *Monascus filiformis* (Rudolphi).
Steringophorus furciger (Olsson).
Steringotrema ovacutum (Lebour).
Steringotrema pagelli (van Beneden).
Microstomus kitt (Walbaum) : *Steringophorus furciger* (Olsson).
Steringotrema pagelli (van Beneden).
Pleuronectes platessa Linnaeus : *Steringophorus furciger* (Olsson).
Steringotrema pagelli (van Beneden).
Reinhardtius hippoglossoides (Walbaum) : *Steringophorus furciger* (Olsson).

Order Lophiiformes
Lophius piscatorius Linnaeus : *Steringophorus furciger* (Olsson).

Acknowledgements

The authors are especially grateful to Mr J. Thulin, University of Gothenburg, Sweden, for generously lending us his valuable collection of fellodistomids, without which this contribution would have been much less complete. We would also like to thank the following: Dr A. V. Gaevskaja, AtlantNIRO, Kaliningrad, USSR, for presenting to us and examining for us specimens of *Pronoprymna;* Dr L. Margolis, Pacific Biological Station, Nanaimo, Canada, for lending specimens of *Pronoprymna* and *Bacciger*; Dr C. R. Kennedy, University of Exeter, for donating specimens of *Pronoprymna*; Professor J. Llewellyn, University of Birmingham, and Dr F. R. Stranack, Portsmouth College of Technology, for lending specimens of *Proctoeces;* Dr R. A. Campbell, Southeastern Massachusetts University, North Dartmouth, USA, for lending specimens of *Abyssotrema*; Dr F. Gudmundsson, Museum of Natural History, Reykjavik, Iceland, for lending the specimen of *Yamagutia*; and both Dr R. A. Matthews, Plymouth Polytechnic, for examining *Atherina* for *Bacciger* and Mrs E. A. Harris, British Museum (Natural History), for attempting to find specimens of *Scrobicularia* infested with *Proctoeces* on our behalf.

We are also indebted to the following: Mr A. C. Wheeler, British Museum (Natural History), for permission to dissect fishes in the Museum's collection; Mr D. W. Cooper and Mr S. J. Moore, British Museum (Natural History), for the preparation of serial sections; the staff of the MAFF Fisheries Laboratory, Lowestoft, and the crew of the RV *Cirolana* for their help to one of us (R. A. B.) on various cruises; the Staff of the Marine Biological Association Laboratory, Plymouth, for help to one of us (D. I. G.) during visits in 1972; and the Staff of the Parasitology Section, DAFS Marine Laboratory, Aberdeen, for their kind help to both of us during visits in 1973 and 1977.

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Manuscript accepted for publication 14 February 1979